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Neogene Paleontology in the northern Dominican Republic

3. The Family Poritidae (Anthozoa: Scleractinia)

by

Ann Budd Foster

Paleontological Research Institution
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Ithaca, New York, 14850 U.S.A.

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CONTENTS

Page

Abstract 47
Resumen 47
Introduction 48
Acknowledgments 49
Abbreviations of Repository Institutions 49
Biostratigraphy and Paleoecology 50
Taxonomic Method
  Problem 56
  Material 59
  Characters 59
  Statistical Procedures 63
  Results and Interpretations 68
  General Comparisons with Other Faunas 70
Systematic Paleontology
  Introduction 73
  Family Poritidae Gray, 1842 74
    Genus *Porites* Link, 1807 75
      Porites baracoaensis Vaughan, 1919 75
      Porites convivatoris, n. sp. 76
      Porites macdonaldi Vaughan, 1919 78
      Porites portoricensis (Vaughan, 1919) 79
      Porites waylandi, nom. nov. 81
    Genus *Goniopora* Blainville, 1830 83
      Goniopora hilli Vaughan, 1919 83
      Goniopora imperatoris Vaughan, 1919 85
      Goniopora calhounensis Weisbord, 1971 87
    Genus *Alveopora* Blainville, 1830 88
      Alveopora tampae Weisbord, 1973 88
Appendix Ia. Means of all corallite characters in the five species of *Porites* herein described 89
Appendix Ib. Means of all corallite characters in the three species of *Goniopora* herein described 89
Appendix IIa. Canonical discriminant analysis of *Porites* groups 2 and 4 90
Appendix IIb. Canonical discriminant analysis of *Porites* groups 1, 3, and 5 90
Appendix IIc. Canonical discriminant analysis of *Goniopora* groups 1 and 2 90
Appendix IId. Canonical discrimination analysis of five fossil and six modern Caribbean species of *Porites* 90
References Cited 91
Explanations of Plates 94
Index 118

LIST OF ILLUSTRATIONS

Text-figure — Page

1. Map indicating the location of the river sections sampled 50
2. Bar charts summarizing the quantity of material collected 51
3. Diagrams showing the distributions of species within selected river sections 52
4. *Porites.* Variation within species in corallite characters through a composite of the Río Cana and Río Gurabo stratigraphic sections 54
5. *Porites.* Variation within species in colony shape through the composite stratigraphic section shown in Text-figure 4 55
6. *Goniopora.* Variation within species in corallite characters and colony shape through the composite stratigraphic section shown in Text-figure 4 57
7. Scanning electron microscope photographs of modern *Porites astreoides* from different reef habitats near Discovery Bay, Jamaica 58
8. Drawings showing some of the characters measured 61
9. Serial acetate peels down one corallite of *Porites furcata* 62
10. *Porites.* Canonical discriminant analysis of the NMB collections 64
11. *Goniopora.* Canonical discriminant analysis of the NMB collections 65
12. *Porites* subgroups. Canonical discriminant analysis of the NMB collections 66
13. *Goniopora* subgroup. Canonical discriminant analysis of the NMB collections 67
14. Means and standard deviations for eight characters in the five *Porites* species 68
15. Means and standard deviations for eight characters in the three *Goniopora* species 69
16. Classification of Neogene Mediterranean types using the canonical discriminant analyses of the NMB collections 72
17. *Porites.* Canonical discriminant analysis of the NMB fossil collections and six modern Caribbean species 73
18. Surface of a modern colony of *Porites astreoides* having a *Synaraea*-like appearance 78
19. Surface of a modern colony of *Porites astreoides* with flaky septa 80

LIST OF TABLES

Table — Page

1. List of Neogene Caribbean poritid types used in statistical analyses 60
2. List of Neogene Mediterranean poritid types and modern Caribbean specimens used in statistical analyses 62
3. List and description of corallite characters analyzed in *Porites* .... foldout inside back cover
4. List and description of corallite characters analyzed in *Goniopora* .... foldout inside back cover
5. Weighting of characters in the all *Porites* canonical discriminant analysis 63
6. Weighting of characters in the all *Goniopora* canonical discriminant analysis 67
7. List of all valid poritid species from the Miocene through lower Pliocene of the Caribbean, showing their current taxonomic status 74

NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC
3. The Family Poritidae (Anthozoa: Scleractinia)

By

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ABSTRACT

Various multivariate statistical procedures are used to distinguish species in the reef-coral family Poritidae through a continuous Neogene sequence (five myr time interval) in the Cibao Valley of the northern Dominican Republic. Some older (by approximately 10 myr) material from the same region is also included in the analyses. The material consists of approximately 450 colonies (120 of which are measured) from 92 localities in four river sections. The colonies are first sorted into three genera, and approximately 30 characters measured on five calices per colony. The data are analyzed using cluster and canonical discriminant analyses to group the colonies into clusters representing species. Five species are so defined in *Porites* and three in *Goniopora.* These groupings are then used statistically to reclassify type specimens for 22 of the 25 described species of Neogene Caribbean poritids. Eight described species are thereby synonymized with four previously-described species in *Porites* and one new species of *Porites, Porites convivatoris,* n. sp., is discovered. Five described species are synonymized with two previously-described species in *Goniopora.* The stratigraphic range of three species of *Porites* and three species of *Goniopora* is also shown to extend back to the late Oligocene, thereby diminishing the significance of any presumed early Miocene adaptive radiation. Only one species was found to be endemic to the Dominican Republic and only one confined to the northern Caribbean. The rest are widely distributed throughout the Caribbean. Thus, the endemism previously believed common during the Neogene is shown to be far less extensive.

Evolutionary trends within each species are preliminarily analyzed for various characters using nonparametric statistical procedures. In general, the results show that seven species experienced little or no evolutionary change (= stasis) through the sequence. Slight increases in corallite size are detected in two species, an increase in colony height in one species, and a more rounded colony shape in one species. These trends may be related to the general deepening of the environment; however, little correlation is found between lithology and morphology within species. Preliminary analyses of the relationship between intraspecific variation and poritid abundance and diversity yield significant results, suggesting that intraspecific trends may be environmental and that future study of coral species associations may offer insight into paleoenvironmental interpretations.

Statistical comparisons with the Miocene Mediterranean poritids show that no species co-occur in the two provinces during the Neogene. Similarly, none of the studied Neogene species of *Porites* resemble modern Caribbean species of *Porites,* signifying that all nine poritid species studied must have become extinct and the modern Caribbean species of *Porites* radiated during the late Pliocene or early Pleistocene.

This study represents part of a multidisciplinary project on the stratigraphy of the northern Dominican Republic, coordinated by P. Jung and J. B. Saunders of the Naturhistorisches Museum Basel, Switzerland.

RESUMEN

Se usan varios procedimientos estadísticos multivariados para distinguir especies de la familia de corales arrecifales Poritidae a travéz de una secuencia Neogéna contínua (intervalo de tiempo de cinco millones de años) en el valle Cibao, al norte de la República Dominicana. Algun materiel de mayor edad (aproximadamente 10 millones de años) de la misma region es tambien incluyendo en las analises. El material consiste en aproximadamente 450 colonias (120 de las cuales son medidas) de 92 localidades en cuatro secciones del río. Primero las colonias son divididas en tres géneros y aproximadamente unos 30 caracteres son medidos en cinco cálices por colonia. Los datos se analizan usando análisis de grupos y análisis canónicos discriminativos para agrupar las colonias en grupos representantes de especies. Cinco especies se definen asi en *Porites* y tres en *Goniopora.* Estas agrupaciones son luego usadas estadísticamente para reclasificar clases de especímenes de 22 de las 25 especies descritas de poritidos Neogénos del Caribe. Ocho especies descritas son comparadas análogamente con cuatro especies previamente descritas en *Porites,* y una nueva especie de *Porites, Porites convivatoris,* n. sp., es descubierta. Cinco especies descritas son comparadas análogamente con dos especies previamente descritas en *Goniopora.* Se ha demonstrando que el alcance estratigráfico de tres especies de *Porites* y tres especies de *Goniopora* se extiende hasta el Oligoceno tardío, disminuendo de ese modo, la importancia de la presumible radiación temprana adaptiva Miocena. Se encontró que solo una especie es endemica de la República Dominicana y que solo una especie fue limitada al norte del Caribe. El resto está distribuído ampliamente a travéz del Caribe. Por lo tanto, la endemia que previamente se consideró común durante el Neogéno, ha demonstrando ser mucho menos extensa.

Las tendencias evolutivas dentro de cada especie son analizadas preliminarmente por varios caracteres usando procedimientos estadísticos no paramétricos. En general, los resultados muestran que siete especies experienciaron poco a ningún cambio evolutivo (estásis) a travéz de la secuencia. Se detectan pequeños aumentos del tamaño de los esqueletos de pólipos en dos especies, un aumento de la altura de la colonia en una especie, y una forma mas redondeada de la colonia en una especie. Estas tendencias podrían estar relacionadas con la profundización general del medio ambiente, sin embargo, se encontró poca correlación en una

escala mas pequeña entre litologia y morfología entre las especies. Análisis preliminares de la relación entre variación intraespecífica y abundancia y diversidad porítida producen resultados importantes que sugieren que las tendencias entraespecíficas podrían ser ambientales y que el estudio futuro de las asociaciones de las especies de corales podría ofrecer un entendimiento de las interpretaciones paleoambientales.

Comparaciones estadísticas con los poritidos Mediterráneos del Mioceno muestran que ninguna especie co-ocurre en las dos provincias durante el Neogéno. En forma similar, ninguna de las especies Neogénas estudiadas de *Porites* se parece a las especies de *Porites* del Caribe moderno, lo cual significa que todas las nueve especies referidas ya estudiadas deben haberse vuelto extinctas y que las especies de *Porites* del Caribe moderno fueron radiadas durante el Plioceno tardío o Pleistoceno temprano.

Este estudio representa parte de un proyecto multidisciplinario de la estratigrafía del norte de la República Dominicana coordinado por P. Jung and J. B. Saunders, Naturhistorisches Museum Basel, Switzerland.

INTRODUCTION

General surveys of taxonomic distributions suggest that a major extinction event occurred in the evolution of Caribbean reef-corals during the late Oligocene. This event was followed by a smaller radiation of taxa in the early Miocene. Many modern coral taxa are believed to have originated during this radiation, together with numerous endemic short-lived Neogene corals that gradually became extinct during Pliocene and early Pleistocene time (Frost, 1977a, 1977b). However, the detailed evolutionary patterns of the radiation and subsequent decline are poorly documented, largely because the definition and evolutionary patterns of many species are based only on a few, poorly-preserved specimens. In addition, the stratigraphic relationships between many coral faunas are known only on a gross scale involving the correlation of several widely-separated sections. The purpose of the present investigation is to redefine Neogene coral species using material collected at regular stratigraphic intervals through a long, continuous sequence. The species redefinitions are made by analyzing morphologic variation in groups of specimens. Emphasis is placed on tracing evolutionary patterns within each species in detail and using the results of this analysis to postulate possible evolutionary relationships. The present study is preliminary in nature and is intended to provide the basis for a more complete systematic revision of all Caribbean Tertiary corals.

This paper is the first in a series of coral faunal descriptions of the middle Miocene to middle Pliocene of the northern Dominican Republic. The coral collections were made between 1978 and 1980 by J. Geister, P. Jung, J. B. Saunders and coworkers as part of their large-scale multidisciplinary project on the paleontology and stratigraphy of the Neogene of the Cibao Valley region, and all collecting localities are keyed into their detailed stratigraphic sections (Saunders *et al.*, 1982; Saunders, Jung, and Biju-Duval, 1986). The project involves specialists on a wide variety of taxonomic groups working on material from the same localities. Therefore, coral evolutionary patterns can eventually be compared with those of other taxa, and ecological and stratigraphic relationships can be interpreted using a large comprehensive data set. Microfossil dates are also available for almost all localities. The collections themselves were made in bulk at regular stratigraphic intervals, offering a rare opportunity to trace the evolution of large coral populations through a five-million year sequence.

The northern Dominican Republic was selected for study because it represents one of the longest, most continuous, and best-studied sections through Neogene coral deposits in the Caribbean. The corals are also exquisitely preserved. This first coral paper in the series covers the most abundant coral family, the Poritidae. Two genera in this family are discussed in detail, one of which, *Porites* Link, 1807, represents an essential component of modern Caribbean and Indo-Pacific reefs. The other, *Goniopora* Blainville, 1830, became extinct in the Caribbean during the late Pliocene and is represented today only by Indo-Pacific forms. A third poorly-represented genus, *Alveopora* Blainville, 1830, which also occurs today only in the Indo-Pacific and is rarely reported in Caribbean Tertiary deposits, is briefly discussed.

Previous work on the systematics of the Dominican Republic corals has involved only a portion of the fauna and was based on limited material. The first major study describing the Neogene corals (Duncan, 1863, 1864, 1868) was based on the Heneken collection (Heneken, 1853), which is now deposited at the BM(NH). In these publications, Duncan described 48 species (32 of which were new) from the "Nivajé Shale" and the "Silt of the Sandstone plain". Most of these descriptions were based on single specimens or fragments of specimens and were re-interpreted by Vaughan (1919) to represent a total of 28 species, 20 of which were new. Vaughan found only two species described by Duncan to belong to the family Poritidae, *Alveopora fenestrata* Dana, 1846 and *Porites collegniana* Michelin, 1842. Shortly after Duncan's publications, Pourtalès (1875) compiled a list of corals collected by W. B. Gabb (Gabb, 1873; deposited at MCZ and ANSP). The list included 30 taxa, five of which could not be assigned to any species. Only one species belonged to the family Poritidae, *Porites furcata* Lamarck, 1816.

Almost fifty years after these initial works, Vaughan (1919, p. 217) listed 28 coral species in the Maury collection (Maury, 1917; deposited at USNM) from the Neogene of the Dominican Republic. One of these species, *Agaricia dominicensis* Vaughan, 1919, he formally described as new, and six others were cited as new and to be described in a later publication, which never appeared. Two of these six species apparently belonged to the Poritidae, and their descriptions are given in an unpublished manuscript on the Maury collection by Vaughan (date unknown). In 1919, Vaughan and Cooke made large, well-documented collections of well-preserved coral specimens in the Dominican Republic, mainly from Río Yaque del Norte, Río Mao, Río Gurabo, and Río Cana. These are listed by USGS locality number in Vaughan *et al.* (1921, pp. 105–168) and deposited at the USNM. Formal systematic descriptions of this material were never completed. Nine new species were eventually described in Vaughan and Hoffmeister (1925); however, these were based primarily on older material from the Gabb collection and included no species belonging to the Poritidae.

Since Vaughan's work, very little has been done on the Neogene coral fauna of the Dominican Republic. Ramírez (1956) has listed five Neogene coral species from Río Amina of the northern Dominican Republic, and Ricart y Menéndez (1981a, 1981b, 1983) has described skeletal structures in three species of *Antillocyathus* Wells, 1937, from an undisclosed locality in the Dominican Republic. Neither worker has attempted to describe the poritids.

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ABBREVIATIONS OF REPOSITORY INSTITUTIONS

AMNH: American Museum of Natural History, New York, NY, U.S.A.

ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, PA, U.S.A.

BM(NH): British Museum (Natural History), London, England, United Kingdom

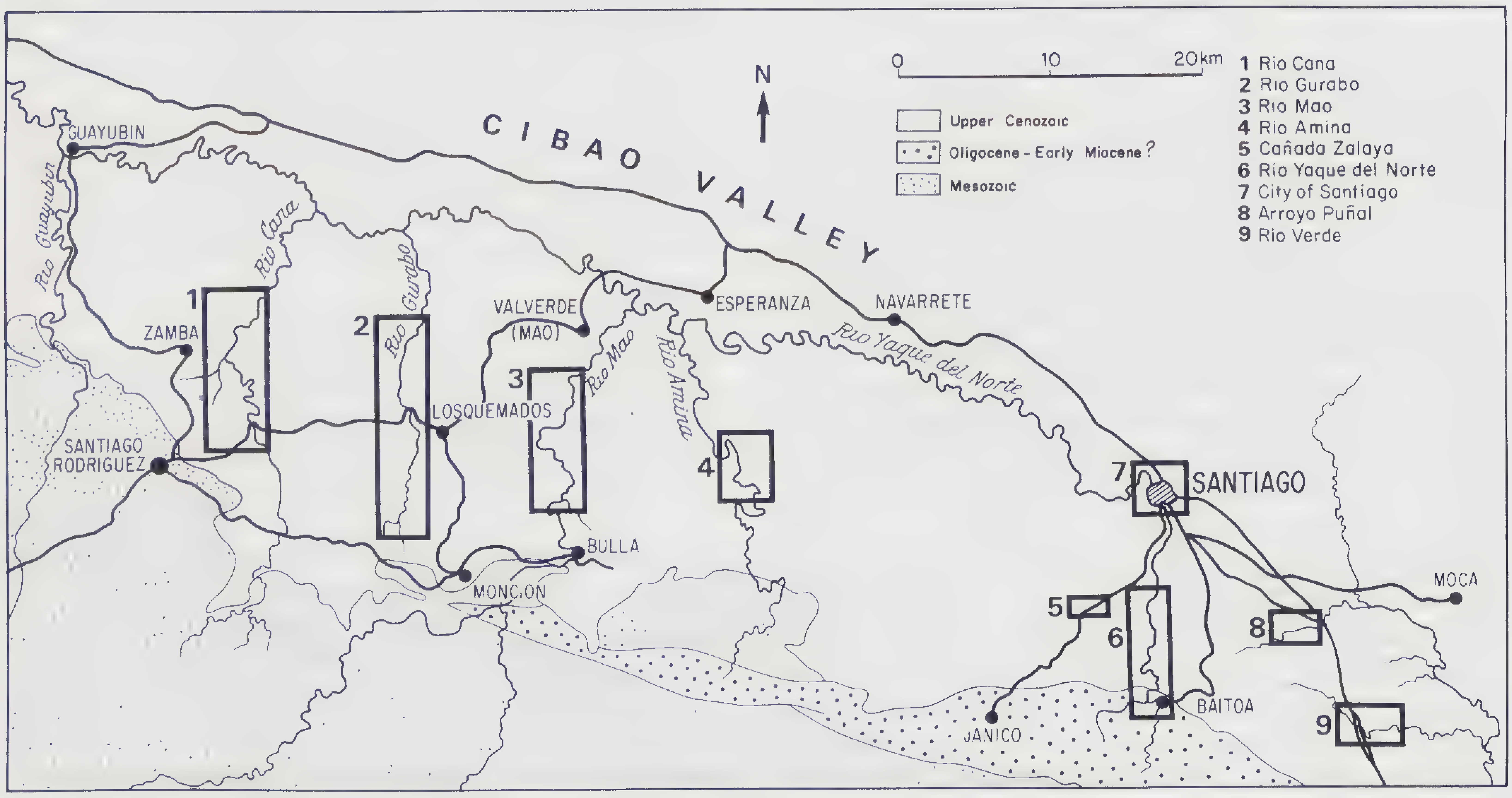
FSU: Florida State University, Department of Geology, Tallahassee, FL, U.S.A.
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.
MHNP: Muséum National d'Histoire naturelle, Paris, France
NHMW: Naturhistorisches Museum Wien, Vienna, Austria
NMB: Naturhistorisches Museum Basel, Switzerland
PIU: Paleontologiska Institutionen Uppsala, Uppsala, Sweden
SUI: State University of Iowa, Iowa City, IA, U.S.A.
UCMP: University of California Museum of Paleontology, Berkeley, CA, U.S.A.
UI: University of Illinois, Department of Geology, Urbana, IL, U.S.A.
USGS: United States Geological Survey, Washington, DC, U.S.A.
USNM: U. S. National Museum of Natural History, Washington, DC, U.S.A. (five-digit catalogue numbers refer to the Department of Invertebrate Zoology, six-digit catalogue numbers refer to the Department of Paleobiology)
YPM: Yale Peabody Museum, New Haven, CT, U.S.A.

BIOSTRATIGRAPHY AND PALEOECOLOGY

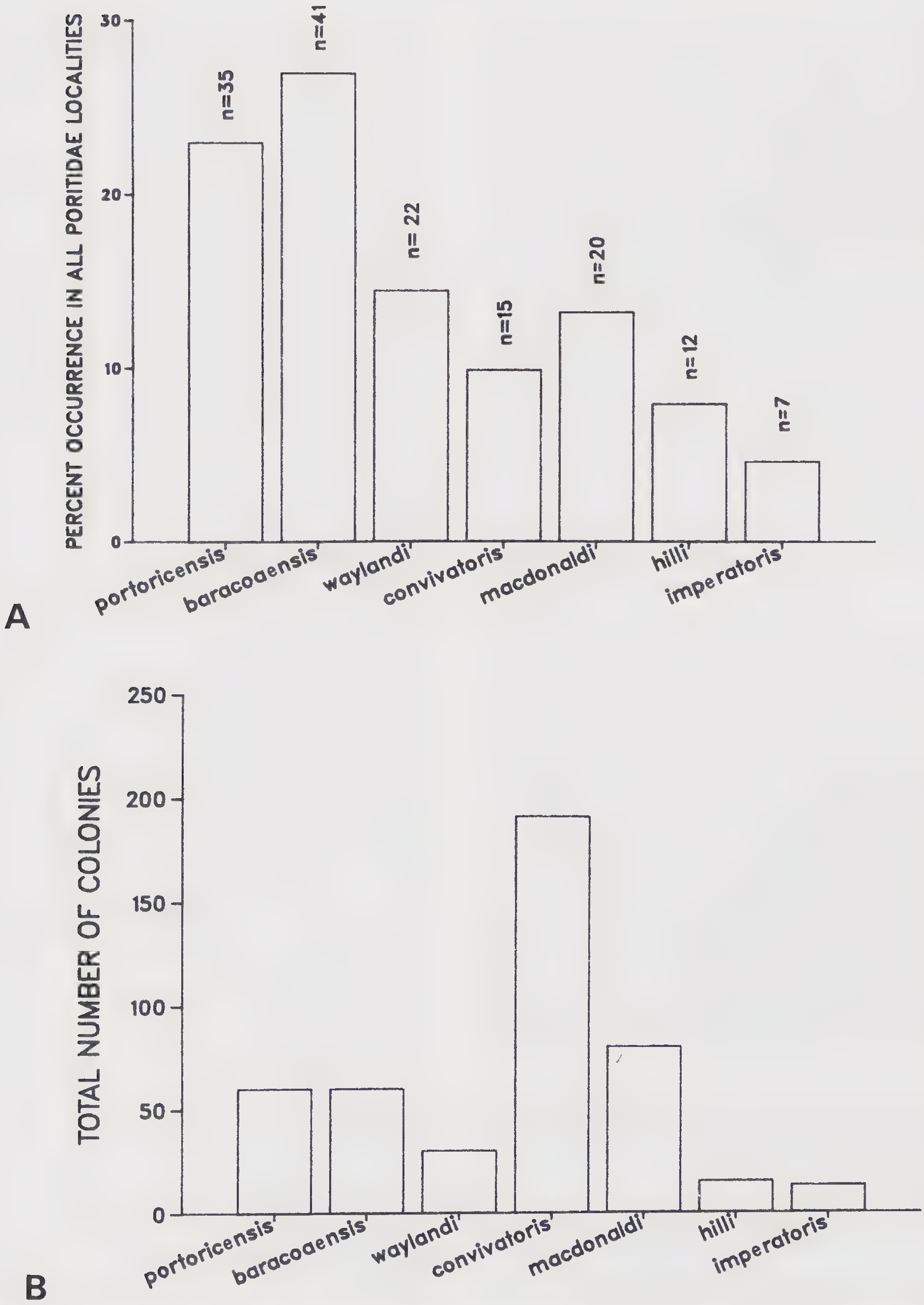
The Poritidae are abundant and widespread in four of the collected river sections (Río Cana, Río Gurabo, Río Mao, and Río Yaque del Norte) of Saunders, Jung, and Biju-Duval (1986) through the Neogene of the Cibao Valley (Text-fig. 1). They were not found elsewhere in the study area. Specimens were collected at a total of 92 localities ranging in age from late Oligocene to middle Pliocene. Two species, *Porites portoricensis* (Vaughan, 1919) and *P. baracoaensis* Vaughan, 1919, are especially prolific, occurring in more than 30 localities each (Text-fig. 2a). *Porites portoricensis* was found in all four river sections (Text-fig. 3), whereas *P. baracoaensis* occurs in all but the older, more conglomeratic Río Yaque del Norte section.

The three remaining species of *Porites* (*P. waylandi,* nom. nov., *P. convivatoris,* n. sp., and *P. macdonaldi* Vaughan, 1919) were collected in 15 or more localities each (Text-fig. 2a). Of these three species, *P. waylandi* was found in all but the Río Mao section. It appears to be more common in the Río Yaque del Norte section and the lower parts of the Río Gurabo and Río Mao sections. *Porites convivatoris* is restricted to the Upper Miocene and Lower Pliocene of the Río Cana and Río Mao sections. *Porites macdonaldi* occurs most commonly throughout the middle portions of the Río Gurabo section and has only a limited distribution along Río Cana and Río Mao (Text-fig. 3).

Goniopora Blainville, 1830 and *Alveopora* Blainville, 1830, were less commonly found (Text-fig. 2a). Of the three species of *Goniopora, G. hilli* Vaughan, 1919 occurs most frequently. It was found in all but the Río Mao section and appears to be restricted to Upper Miocene (possibly lowermost Pliocene) and older sediments. *Goniopora imperatoris* Vaughan, 1919



Text-figure 1.—Map indicating the location of the river sections sampled. Members of the Poritidae were found only in four sections: (1) Río Cana, (2) Río Gurabo, (3) Río Mao, and (6) Río Yaque del Norte (map from Saunders, Jung, and Biju-Duval, 1986).



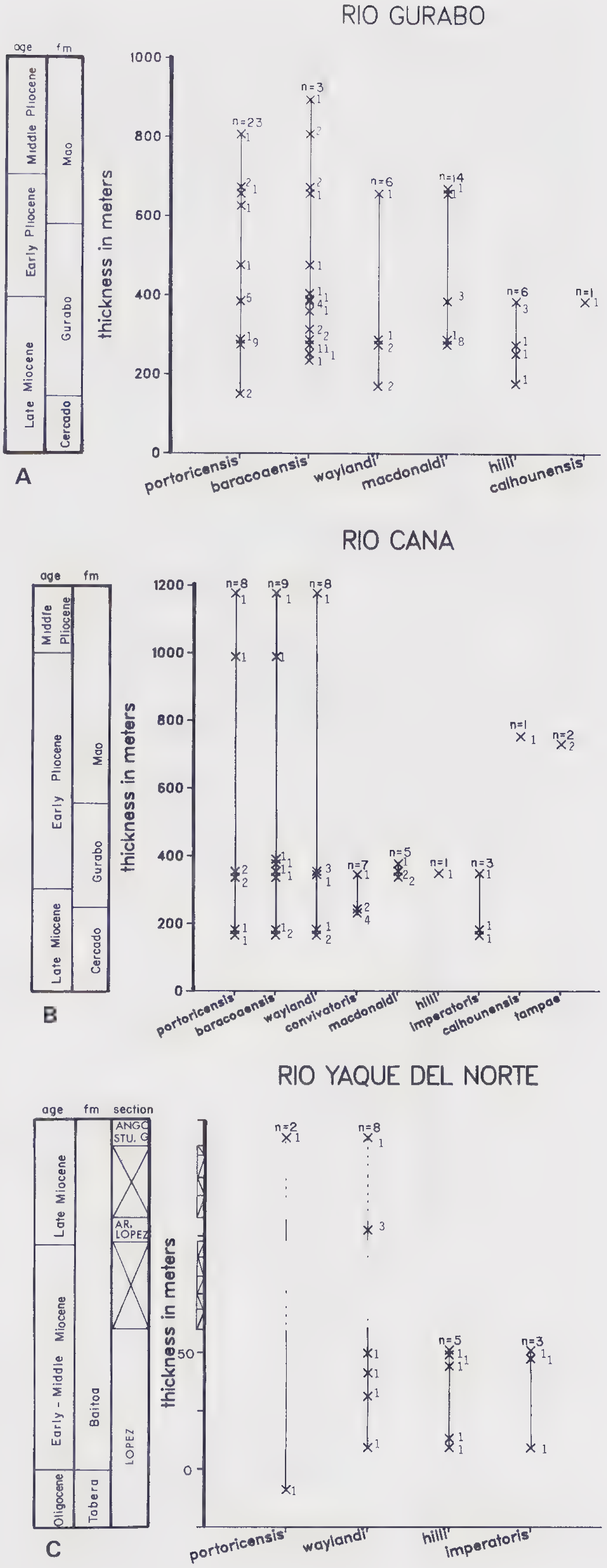
Text-figure 2.—Bar charts summarizing the quantity of material collected. (A) Percentage of all Poritidae localities containing each species. "n" = total number of localities represented. (B) Total estimated number of colonies collected of each species.

occurs in all but the Río Gurabo section and seems to be restricted to sediments of the same age as *G. hilli. Goniopora calhounensis* Weisbord, 1971 was found only at two localities (one on Río Cana and the other on Río Gurabo), both of which are relatively high in the section (Text-fig. 3). *Alveopora* only rarely occurs in the region studied and is represented by one species (*A. tampae* Weisbord, 1973). It is confined to the Upper Oligocene Tabera Group (Text-fig. 3b).

The overall abundance of the seven common poritid species in the NMB collections cannot be determined with any accuracy. Numbers of individuals (*i.e.,* colonies) cannot be directly counted with certainty, because the specimens are so severely fragmented. Volumetric estimates do not reflect the genetic structure of the population, because of extensive differences in adult size and reproduction (especially, the relative contribution of asexual vs. sexual reproduction) between coral species. These difficulties are best demonstrated by the three following examples. First, specimens of the two branched species (*P. portoricensis* and *P. baracoaensis*) consist of numerous broken fragments, from which it is impossible to reconstruct the original colonies. In such cases, it is conceivable that all the pieces of a species from one locality belonged to the same colony or at least the same clone. Second, even large, massive corals such as *G. hilli* are often so badly broken that it is difficult to determine which pieces belonged to the same colony. Third, *P. convivatoris,* which formed small, compact colonies, is usually preserved unbroken and is represented by numerous countable individuals at several localities (*e.g.,* 83 colonies at NMB loc. 16928). Because of its small size, however, *P. convivatoris* is not volumetrically important in any NMB sample.

In light of these problems, to describe abundance, the number of colonies of each species has only been subjectively estimated, and the general results are graphed on Text-figure 2b. *Porites convivatoris* is represented by the greatest number of colonies and the two species of *Goniopora* by the least. The remaining four species of *Porites* have roughly equivalent values, with *P. waylandi* possibly having the fewest individuals.

Study of patterns of morphologic variation across a composite of the Río Cana and Río Gurabo stratigraphic sections (spanning a time interval of approximately five myr) shows pronounced stability within each species (Text-figs. 4, 5, 6). Variability within



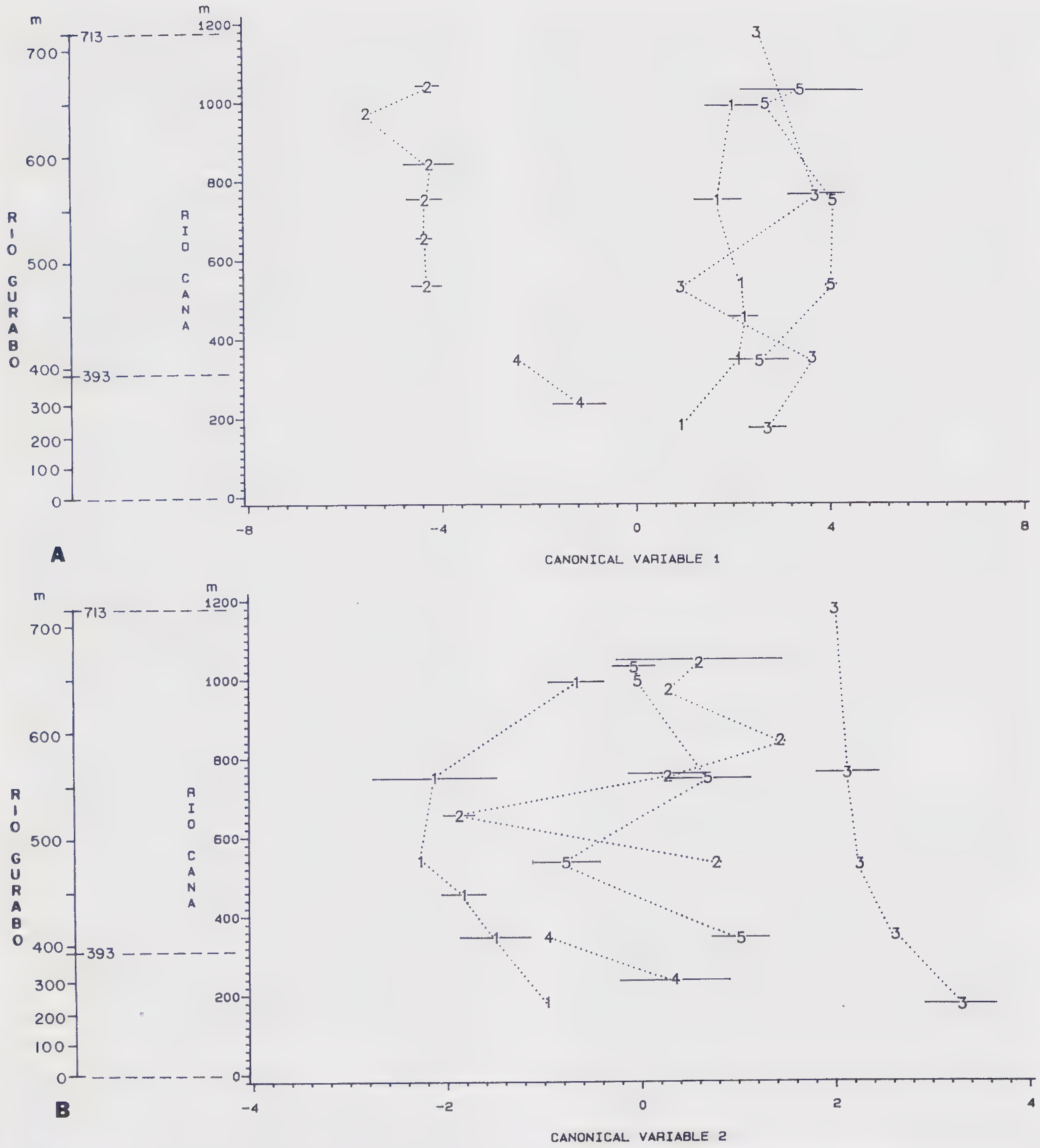
Text-figure 3.—Diagrams showing the distributions of species within selected river sections. "n" = total number of localities containing each species. Numbers to the right of points along each vertical distribution line indicate the number of localities represented by each point. (A) Río Gurabo, (B) Río Cana, (C) Río Yaque del Norte.

species is indeed high within many stratigraphic intervals, but overall change upsection within each species is only slight or nonexistent. This general result is confirmed by a Runs statistical test and a Binomial statistical test performed on 50-m and 100-m interval time series data for each species using the SPSS-X NPAR procedure (SPSS Inc., 1983). In all five species of *Porites,* canonical variable 1 (a variable describing corallite wall structure and corallite spacing; see description of all *Porites* canonical discriminant analysis in the next section) remains unchanged upsection (Text-fig. 4a). Results of regression analysis and Spearman's rank order correlation coefficients (SAS Inst., 1982, PROC REG and PROC CORR) indicate that no relationship or correlation exists between relative stratigraphic position and this canonical variable. However, canonical variable 2 of the same canonical analysis (a variable describing the inverse of corallite size) does appear to decrease upsection in *P. waylandi* (r_S = −0.750, p = 0.012). Values of canonical variable 2 for the remaining four species (*Porites portoricensis, P. baracoaensis, P. convivatoris* and *P. macdonaldi*) all zigzag back and forth upsection without any detectable overall trend (Text-fig. 4b). Colony shape also does not appear to change upsection. Spearman's rank order correlation coefficients show insignificant correlations between stratigraphic position and branch thickness in the two branching species of *Porites* (Text-fig. 5a), and between stratigraphic position and the ratio of colony height to length in the three massive species of *Porites* (Text-fig. 5b). In the two species of *Goniopora,* significant directional changes occur upsection only in colony shape (r_S = 0.580, p = 0.002) of *G. imperatoris* (Text-fig. 6) and in colony height of *G. hilli* (r_S = −0.717, p = 0.0004). Significant differences in canonical variable 1 (a variable describing corallite size; see *Goniopora* canonical discriminant function analysis in the next section) occur also between specimens of *G. hilli* collected on Río Yaque del Norte and those collected on Río Cana and Río Gurabo using two nonparametric rank sum statistical tests, the Wilcoxon 2-sample test (p = 0.0414) and the Kruskal-Wallis test (p = 0.0311), of the SAS NPAR1WAY procedure (SAS Inst., 1982).

This general stability suggests not only a lack of evolutionary development but also a lack of response to environmental change, since the Cibao Valley Neogene section is believed to have been deposited under gradually deepening conditions (Saunders, Jung, and Biju-Duval, 1986). It is unclear if the slightly increased corallite sizes in *P. waylandi* and *G. hilli,* and larger, more rounded colony shape in *G. imperatoris* and *G. hilli* are caused genetically or environmentally. Spearman's rank order correlation coefficients show that lithology is not simply correlated with canonical variable 1, canonical variable 2, or colony size or shape in any of the examples above. This lack of correlation may be partially related to the fact that many of the corals in this study were found in transported rubble layers within silts. However, significant correlations with the diversity and abundance of poritid species collected at each locality do exist in some instances, suggesting that some intraspecific trends may be environmental. For example, canonical variable 2 (a variable describing corallite size; see description of all *Porites* canonical discriminant analysis in the next section) is positively correlated with abundance (*i.e.,* number of poritid colonies collected per locality) in *P. waylandi* (r_S = 0.700, p = 0.004). Decreases in thickness of plates of *P. macdonaldi* (r_S = −0.532, p = 0.041) and more rounded shapes in *P. waylandi* (r_S = 0.512, p = 0.051) appear correlated with increased number of species. Flatter, more encrusting colonies are correlated with increased diversity (calculated using the Simpson diversity index as given in Pielou, 1969) in both *G. hilli* (r_S = −0.790, p = 0.0001) and *G. imperatoris* (r_S = −0.565, p = 0.0001). Assuming that abundance and diversity of the collected poritids are related to reef development, these preliminary results suggest that study of variation in some massive species (especially in colony size and shape) may be potentially useful in interpreting subtle changes in environment upsection. The details of this relationship, however, can only be further explored when occurrence data are compiled for more taxa through the studied stratigraphic sections.

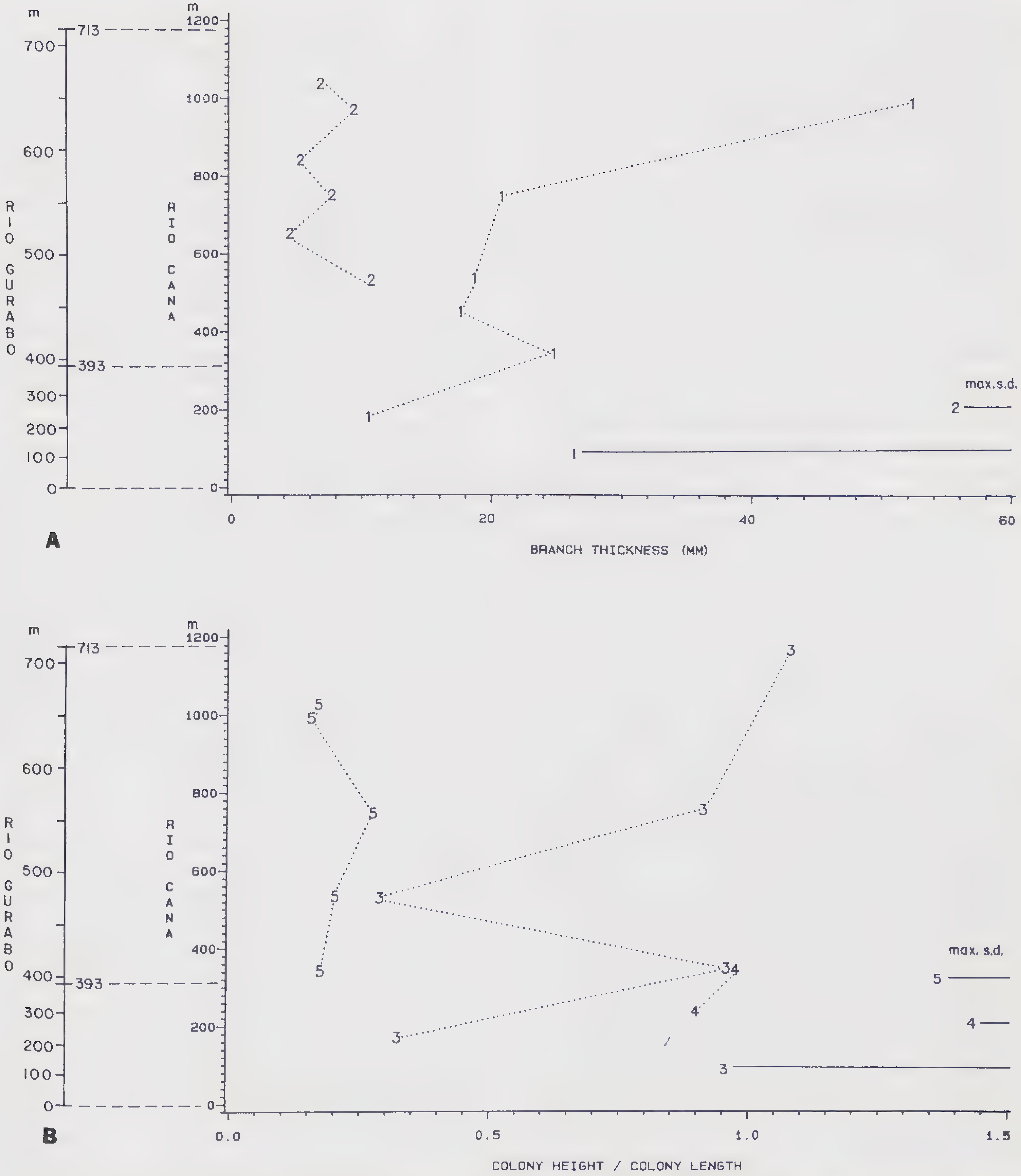
Distribution patterns for occurrences of single species offer less paleoecological potential. The collected poritid species do not appear to be confined to any one lithology, although some limitations have been observed. *Porites baracoaensis* does not occur in the conglomerates at the base of the series, whereas *P. waylandi* and the two abundant species of *Goniopora* occur more commonly there. The restriction of *P. convivatoris* to a few isolated pockets in the silts of Río Cana and Río Mao is especially enigmatic and may be related to reproduction, recruitment, its possible symbiont, or other biological factors unrelated to the physical environment.

Few paleoecological interpretations can be deduced by directly comparing these fossil species with modern analogs. None of the poritid species collected during the study exist today or have direct modern counterparts (see p. 71). All three genera occur today in a wide variety of reef habitats. *Porites,* especially, is widely distributed across modern reefs and occurs from shallow nearshore zones across the lagoon and reef crest into the deep forereef areas. Furthermore, with the exception of *P. convivatoris, G. calhounensis,* and *Al-*



Text-figure 4.—*Porites.* Variation within species in corallite characters through a composite of the Río Cana and Río Gurabo stratigraphic sections. The composite was constructed using the Río Cana section (Saunders, Jung, and Biju-Duval, 1986, text-fig. 16) as a standard and scaling the Río Gurabo section (Saunders, Jung, and Biju-Duval, 1986, text-fig. 6) relative to it. To accomplish this, three exact elevations were correlated between the two sections: (1) the unconformity with the Tabera Group at the base of each section, (2) the boundary between the *Globorotalia humerosa* and *G. margaritae* foraminiferal zones, and (3) the boundary between the *G. margaritae* and *G. miocenica* zones. The positions of localities within each section were determined using text-figures 4 and 15 of Saunders, Jung, and Biju-Duval (1986).

The points (labelled 1–5) on the diagram above represent means for every 100-meter interval along the composite section. 1 = *P. portoricensis,* 2 = *P. baracoaensis,* 3 = *P. waylandi,* 4 = *P. convivatoris,* 5 = *P. macdonaldi.* Horizontal lines on either side of each point are one-half standard deviation in length. (A) Canonical variable 1 of the all *Porites* canonical discriminant analysis. As described in the following section,



Text-figure 5.—*Porites.* Variation within species in colony shape through the composite stratigraphic section shown in Text-figure 4. 1 = *P. portoricensis,* 2 = *P. baracoaensis,* 3 = *P. waylandi,* 4 = *P. convivatoris,* 5 = *P. macdonaldi.* The lengths of the maximum standard deviation are given. (A) The three massive species of *Porites.* (B) The two branching species of *Porites.*

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wall structure and calice elevation are most heavily weighted on this canonical variable. (B) Canonical variable 2 of the all *Porites* canonical discriminant analysis. The inverse of corallite diameter is heavily weighted on this canonical variable. The lengths of the maximum standard deviation are given.

veopora tampae, all the poritids in the study have wide biogeographic distributions across the Caribbean throughout Neogene time. However, the local distribution patterns and morphologic variation have not been studied adequately at other Neogene Caribbean localities (especially the type localities for these species) for use in interpreting the patterns observed in this study.

In conclusion, because of the wide ecologic and biogeographic distributions, extensive variability, and the apparent stability of most of the poritid species in the collections of Saunders, Jung, and Biju-Duval (1986), it seems premature to assign to them any biostratigraphic or paleoecologic importance. Their long durations may eventually prove detrimental to their potential biostratigraphic value, and their wide environmental distributions may decrease the paleoecological value of studying the occurrences of individual species. However, preliminary results suggest that (1) patterns of variation within single species and (2) patterns of abundance and diversity for the complete coral fauna may eventually provide important keys to paleoenvironmental interpretation of the sections studied. Since none of fossil species studied have direct modern counterparts and the variability within species does not appear clearly to be correlated with lithology, the true value of studies of intraspecific variation cannot be determined until all the corals in the collections of Saunders, Jung, and Biju-Duval (1986) have been studied taxonomically, and data are available on the distribution and abundance of the complete coral fauna. Interpretations of overall patterns of diversity and abundance for the coral fauna would require: (1) comparisons with other Neogene and modern Caribbean reefs, and (2) substantiation of patterns by analyzing the spacing, size, and arrangement of *in situ* coral colonies at selected localities, as well as by determining whether colonies at these localities are preserved in growth position. Since modern corals appear distributed across reefs in zones composed of unique associations of species (see Geister, 1983), one further possible method for future environmental interpretation using data for the entire coral fauna in the collections of Saunders, Jung, and Biju-Duval (1986) would involve quantitative analyses of associations of species [for example, by procedures similar to reciprocal averaging and correspondence analysis as used by Cisne and Rabe (1978)].

TAXONOMIC METHOD

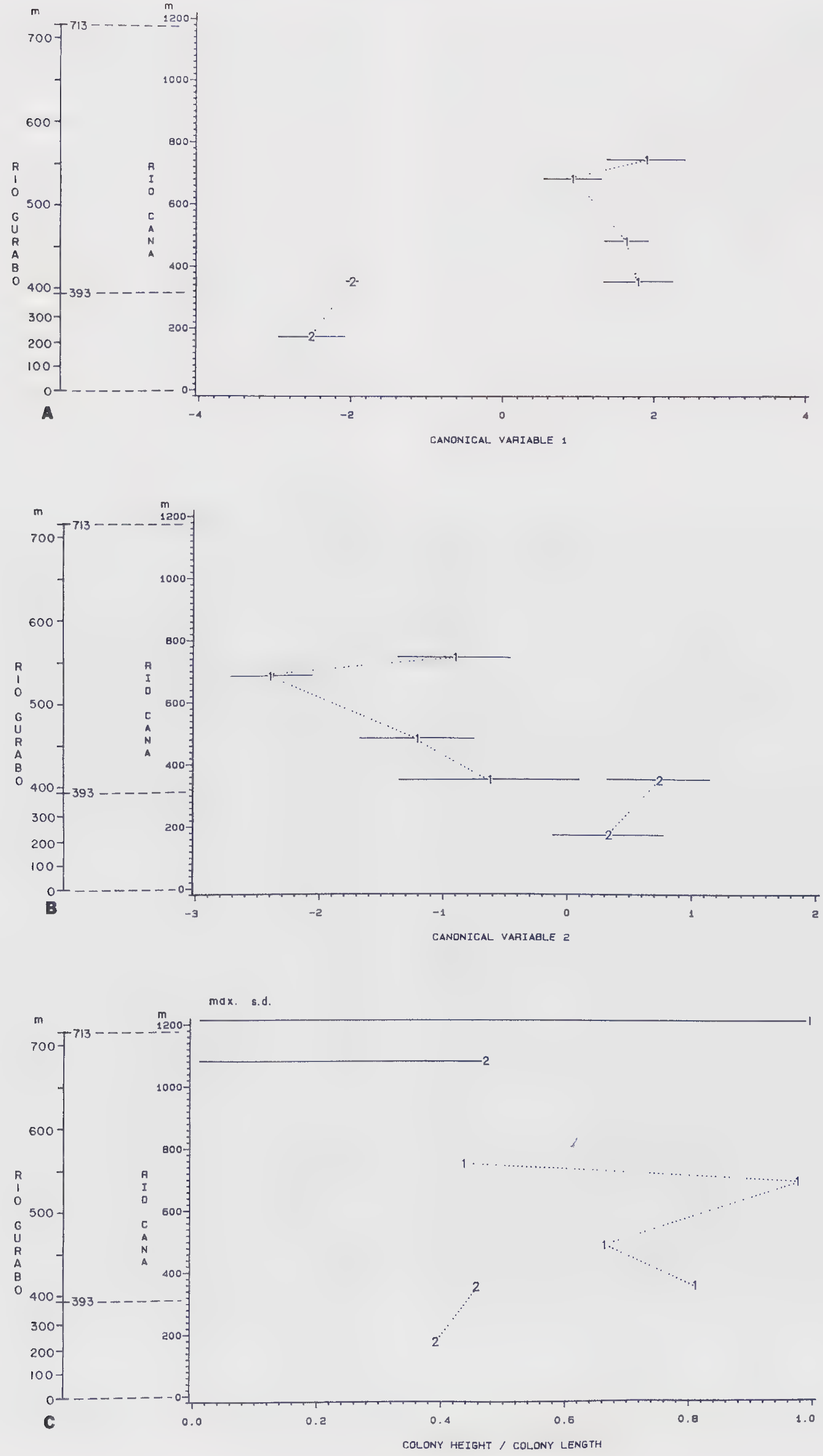
PROBLEM

The Poritidae include many of the most abundant reef-corals throughout the world, since early Neogene time. Yet, because of their extensive variability and relative lack of distinct skeletal features, their taxonomy is highly problematic. As explained by Bernard (1901, 1903, 1905) and reconfirmed by Brakel (1976), the species do not form discrete morphologic clusters but show a gradational continuum in all morphologic characters. This apparent lack of distinct groupings led Bernard to abandon the species concept and Linnean taxonomy altogether (see detailed discussion in Cock, 1977), and it led Brakel to identify only "phenons" in his morphometric study of corallite variation in Jamaican representatives of *Porites* Link, 1807.

In modern Caribbean *Porites,* various interpretations have been proposed to explain the number of species that exist at any one locality (Pl. 15). Several workers have recognized only two species, one massive (*P. astreoides* Lamarck, 1816) and the other branched [*P. porites* (Pallas, 1766)] (see Vaughan, 1901; Cairns, 1982; Roos, 1971; Almy and Carrión-Torres, 1963; Zlatarski and Estalella, 1982). In doing so, they typically synonymize the three branching forms *P. porites, P. furcata* Lamarck, 1816, and *P. divaricata* Lesueur, 1821. Doubt is also expressed as to the validity of *Porites branneri* Rathbun, 1887, which is sometimes believed synonymous with *P. astreoides* Lamarck, 1816 by workers in the Caribbean (*e.g.,* Roos, 1971) but appears to represent a distinct morphologic group in Brazil (Laborel, 1969).

Although some general relationships between colony shape and environment have been observed (Roos, 1967), variation in calice morphology within species is widespread and does not follow any consistent pattern that can be correlated with environmental variables. In *Porites furcata,* for example, skeletal structures appear more heavily calcified, calices shallower, and wall reticula thicker with increased depth on the forereef near Discovery Bay, Jamaica. However, in *Porites astreoides,* calice elevation is deepest and skeletal structures thinnest in low-light environments. Corallite diameter is largest in the backreef and smallest on a nearshore patch reef, both representing shallow, high-light environments with equivalent wave energies (Text-fig. 7). This lack of correlation between calice

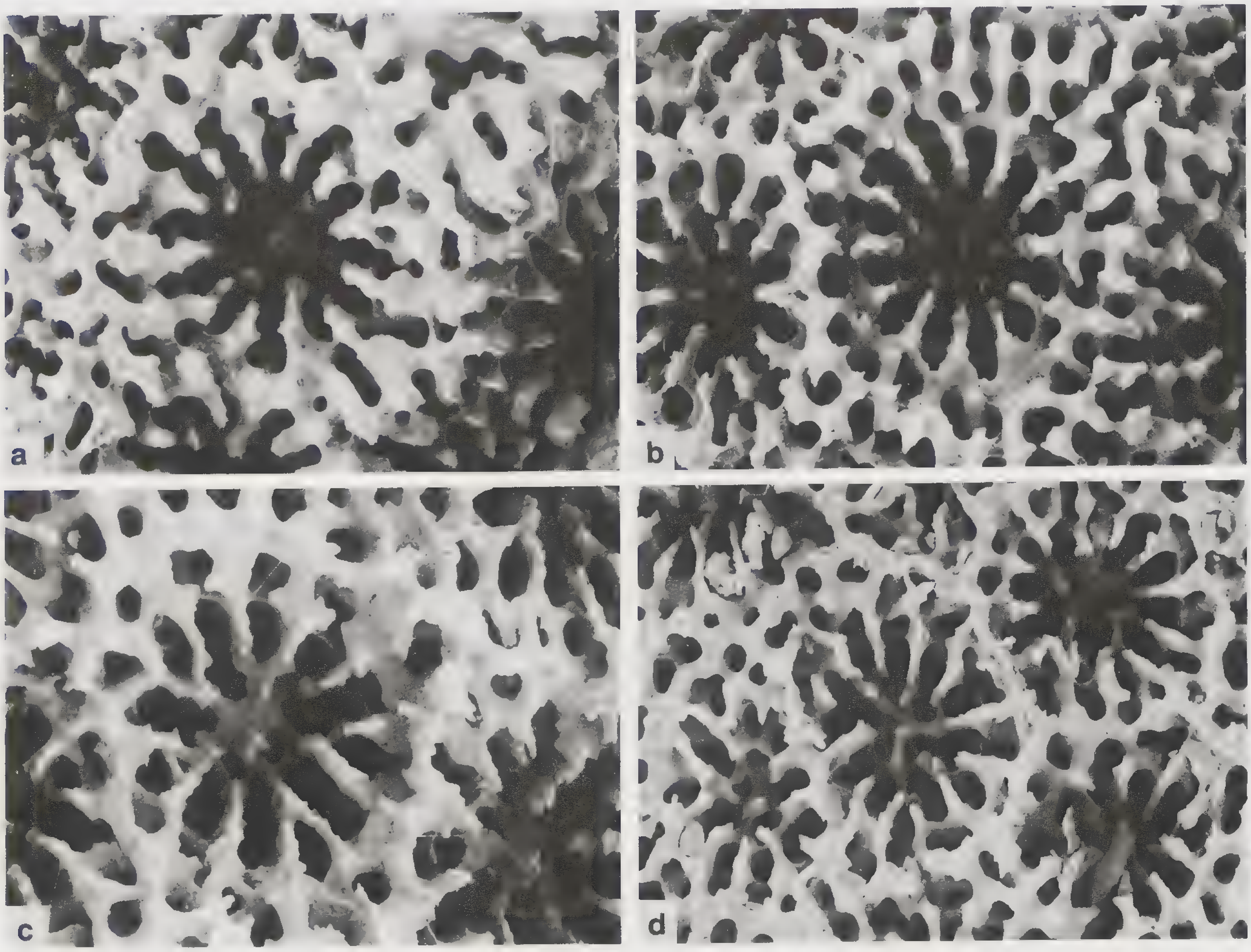
Text-figure 6.—*Goniopora.* Variation within species in corallite characters and colony shape through the composite stratigraphic section shown in Text-figure 4. 1 = *G. hilli,* 2 = *G. imperatoris.* (A) Canonical variable 1 of the all *Goniopora* canonical discriminant analysis. As described in the following section, corallite diameter is most heavily weighted on this canonical variable. Horizontal lines on either side of each point are one-half standard deviation in length. (B) Canonical variable 2 of the all *Goniopora* canonical discriminant analysis. Septal length and elevation are most heavily weighted on this canonical variable. Horizontal lines on either side of each point are one-half standard deviation in length. (C) Colony shape. The lengths of the maximum standard deviation are given.


RIO GURABO
RIO CANA
713
393
A
CANONICAL VARIABLE 1
B
CANONICAL VARIABLE 2
max. s.d.
C
COLONY HEIGHT / COLONY LENGTH

morphology and environmental variables contrasts with the strong correlations found in species of *Montastraea* Blainville, 1830, and *Siderastrea* Blainville, 1830, collected at the same localities (Foster, 1979, 1980). To deal with such complex variation in *Porites,* Vaughan (1907) described 16 forms of Hawaiian *Porites compressa* Dana, 1846 and presented a complex diagram to illustrate their interrelationships. He did not, however, attempt to explain the cause for this variation.

Work on reproduction in modern *Porites* suggests that much intraspecific variability may be directly caused by high genetic variation. In general, *Porites* is especially fecund and reproduces sexually by planulation (Goreau, Goreau, and Hayes, 1981; Kojis and Quinn, 1982). Therefore, a species would not necessarily form a completely coherent morphologic cluster but could include numerous scattered outliers, whose morphologies cannot be explained without knowledge of the underlying genetic controls. This interpretation of widespread genetic variation is also supported by Brakel (1977) in his morphometric analyses of modern *Porites* skeletons.

Given these difficulties in delineating modern species, a relatively objective, statistical approach has been adopted in the present analysis of fossil species. Specimens were subjectively sorted into genera and grouped into clusters using various multivariate analyses of morphometric data. The clusters merely represent concentrations of specimens, which theoretically can overlap at the margins. Since the present work is preliminary, it is possible that some of the marginal specimens may be misassigned to a cluster. The important contribution of this study lies in clearly identifying the



Text-figure 7.—Scanning electron microscope photographs of modern *Porites astreoides* from different reef habitats near Discovery Bay, Jamaica. All photos, ×40. (A) SUI 49915, sand channel (20 m), (B) SUI 47086, lagoon (16 m), (C) SUI 49935, backreef (1 m), (D) SUI 49925, nearshore patch reef (4 m). Study shows that: the wall reticulum is best developed in the lagoon and thinnest in the patch reef, corallite diameter is largest in the forereef and smallest in the patch reef, corallite diameter is largest in the backreef and smallest in the patch reef, calice elevation is deepest in the lagoon and shallowest in the backreef, thickness of septal structures is greatest in the sand channel and smallest in the lagoon and patch reef.

number of groups and their centroids, and roughly estimating the variability of each. Within this framework, all available primary types from the Caribbean Neogene have been re-evaluated. Also possible relationships with modern Caribbean and Neogene Mediterranean species have been postulated.

MATERIAL

The material studied consists of all the specimens of Poritidae (approximately 450 colonies) collected in the Dominican Republic by J. Geister, P. Jung, J. B. Saunders, and other coworkers between 1978 and 1980 (Saunders, Jung, and Biju-Duval, 1986), and is currently deposited at the Naturhistorisches Museum in Basel. These coral collections from the Dominican Republic are termed "NMB" collections in the following discussion in order to distinguish them from other type and comparative material used in the analyses. First, the Poritidae were separated from the rest of the coral collections and sorted into three genera, *Porites, Goniopora* Blainville, 1830, and *Alveopora* Blainville, 1830. The chief characteristic used to distinguish the three genera was septal number and arrangement (see description of septal structure and arrangement in the following section on characters). Specimens assigned to *Porites* had 10 to 14 septa, usually consisting of one directive, a ventral triplet, and four lateral pairs. Specimens assigned to *Goniopora* had 18 to 30 septa arranged in three cycles, the first of which consists of five to eight directives. Specimens assigned to *Alveopora* had weakly-developed septa, not arranged in any definite pattern. The specimens within each genus were then divided into groups on the basis of colony shape and corallite diameter. In this process, 10 groups were distinguished in *Porites* and two in *Goniopora*. Then, 10 to 15 well-preserved specimens from a wide range of localities were selected from each group. These specimens were measured and used in the statistical analyses. A total of 120 NMB colonies were selected and measured.

Measurements were also made on 40 type specimens of 22 of the 25 described species of *Porites* and *Goniopora* from the Neogene of the Caribbean region (Table 1). Types of the remaining three described species, *Goniopora calhounensis* Weisbord, 1971, *Porites chipolanum* Weisbord, 1971, and *Goniopora aucillana* Weisbord, 1973, are currently deposited at Florida State University, Tallahassee, FL, U.S.A., but were not received on loan until after the statistical analyses were completed. In addition to Neogene Caribbean types, specimens of six species of modern *Porites* from the Caribbean region and types of some of the more common Mediterranean Neogene poritid species were measured (Table 2).

Five corallites from various positions within each colony were measured. Previous work (Foster, 1985) has indicated that five is the minimum number of corallites necessary to describe a colony. Since the goal of the present study is essentially exploratory in nature and time was limited, only the minimum number of corallites on the maximum number of colonies were measured. Except where stated, the statistical analyses were performed using colony means of the five corallites. To describe and explain the variation within each taxon in more detail, subsequent measurement of 10 to 15 corallites per colony as well as simulation of original colony form would be necessary.

CHARACTERS

The characters analyzed consist of linear measurements and counts on 29 calice features (Tables 3, 4; Text-fig. 8). All data are available on computer tape from the author. This emphasis on calices rather than colony form follows the suggestion of Brakel (1976) that corallite (not colony) variation is largely genetically controlled. This approach conforms to the practice of Veron and Pichon (1982) in their recent revision of the modern Poritidae of eastern Australia. Study of calice morphology also represents the most consistent way to analyze fossils for which only fragments of the original colony are available for study. Thin-sections of the Poritidae provide few additional characters because calices are typically shallow and not traceable through the corallum.

The characters have been selected to include all diagnostic features used to distinguish modern poritid species in both the Indo-Pacific and Caribbean regions. They can be grouped into five major categories: (1) corallite size and elevation, (2) septal structure and arrangement, (3) development of the pali, (4) size and structure of the columella tubercle, and (5) size and structure of the coenosteal reticulum. Very little is known of the ontogenetic or evolutionary development of these features. Their structure has been described most comprehensively by Bernard (1900, 1903, 1905, 1906). A brief summary is given below:

(1) *Corallite size and elevation.*—As explained above, calices are usually superficial and do not extend deep into the corallum, especially in *Porites*. They are either circular or polygonal, depending on whether or not the wall reticulum (often termed "coenosteal reticulum") is developed. The calice is bilaterally symmetrical. One measure (an average of measurements made parallel and perpendicular to the line of symmetry), **CD**, was analyzed to describe corallite size. Four measures, **CE**, **PE**, **SE**, **WE**, were made to describe overall calice elevation and the elevation of various structures in the calice. Fossa shape and the slope of the septal margins within the calice can be approximated using a combination of these measurements.

Table 1.—List of Neogene Caribbean poritid types used in statistical analyses.

Porites analysis:

1. *Porites carrizensis* Vaughan, 1917, holotype, USNM 68293, USGS locality 7616, Barrett Canyon, San Diego County, California
2. *Goniopora portoricensis* Vaughan, 1919, holotype, USNM 325061, USGS locality 3191, Lares, Puerto Rico
3. *Goniopora portoricensis* Vaughan, 1919, paratype, USNM 325060, USGS locality 3191, Lares, Puerto Rico
4. *Goniopora clevei* Vaughan, 1919, holotype, PIU WI10, Anguilla
5. *Goniopora clevei* Vaughan, 1919, paratype, PIU WI9, Anguilla
6. *Goniopora clevei* Vaughan, 1919, paratype, USNM 325111, USGS locality 6893, Crocus Bay, Anguilla
7. *Goniopora clevei* Vaughan, 1919, paratype USNM 325115, USGS locality 6966, Crocus Bay, Anguilla
8. *Goniopora clevei* Vaughan, 1919, figured specimen, USNM 325116, USGS locality 6016, Empire Quarry, Canal Zone
9. *Goniopora cascadensis* Vaughan, 1919, holotype, USNM 325072, USGS locality 6020c, Las Cascadas, Canal Zone

10–11. *Goniopora cascadensis* Vaughan, 1919, paratypes, USNM 335073, USGS locality 6020c, Las Cascadas, Canal Zone

12. *Porites baracoaensis* Vaughan, 1919, holotype, USNM 325069, USGS locality 3476, Baracoa, Cuba
13. *Porites baracoaensis matanzasensis* Vaughan, 1919, holotype, USNM 325067a, USGS locality 3461, Matanzas, Cuba
14. *Porites baracoaensis matanzasensis* Vaughan, 1919, paratype, USNM 325067b, USGS locality 3461, Matanzas, Cuba

15–16. *Porites douvillei* Vaughan, 1919, original syntypes, USNM 325106 (lectotype designated herein: USNM 325106), USGS locality 6016, Empire Quarry, Canal Zone

17. *Porites toulai* Vaughan, 1919, holotype, USNM 325105a, USGS locality 6016, Empire Quarry, Canal Zone

18–19. *Porites toulai* Vaughan, 1919, paratypes, USNM 325105b, USGS locality 6016, Empire Quarry, Canal Zone

20. *Porites panamensis* Vaughan, 1919, holotype, USNM 325063, USGS locality 6015, Empire Quarry, Canal Zone

21–22. *Porites panamensis* Vaughan, 1919, paratypes, USNM 325064, USGS locality 6016, Empire Quarry, Canal Zone

23. *Porites anguillensis* Vaughan, 1919, holotype, PIU WI43, Anguilla

24–25. *Porites* (*Synaraea*) *howei* Vaughan, 1919, original syntypes, USNM 325113 (lectotype designated herein: USNM 72890), USGS locality 6016, Empire Quarry, Canal Zone

26–28. *Porites* (*Synaraea*) *macdonaldi* Vaughan, 1919, original syntypes, USNM 325046a (lectotype designated herein: USNM 72376), USGS locality 6016, Empire Quarry, Canal Zone

29. *Porites trinitatis* Vaughan, *in* Vaughan and Hoffmeister, 1926, holotype, USNM 353674, USGS locality 8299, Cumuto Road, Trinidad
30. "*Porites floridaprima* Bernard" Weisbord, 1973, topotype, USNM 66220, USGS locality 3286, Tampa, Florida
31. *Goniopora ballistensis* Weisbord, 1973, paratype, USNM 68314, USGS locality 3286, Tampa, Florida
32. *Goniopora matsoni* Weisbord, 1973, holotype, USNM 68315, USGS locality 6546, Tampa, Florida

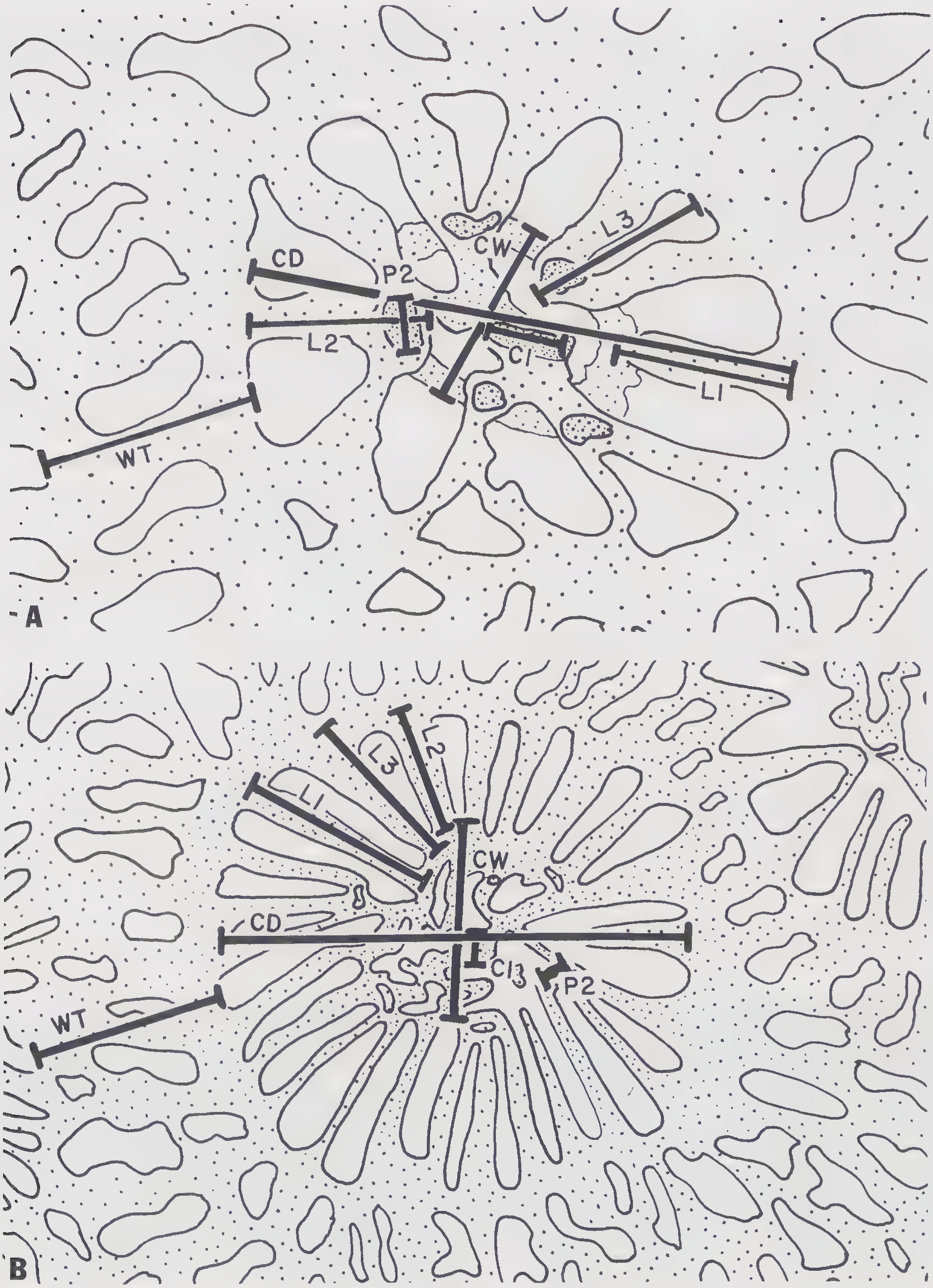
Goniopora analysis:

1. *Goniopora hilli* Vaughan, 1919, holotype, USNM 325058, USGS locality 6016, Empire Quarry, Canal Zone
2. *Goniopora panamensis* Vaughan, 1919, holotype, USNM 325053, USGS locality 6016, Empire Quarry, Canal Zone
3. *Goniopora decaturensis* Vaughan, 1919, holotype, USNM 325031, USGS locality 3383, Hales Landing, Georgia
4. *Goniopora jacobiana* Vaughan, 1919, holotype, USNM 325077, USGS locality 3446, La Cruz, Cuba
5. *Goniopora jacobiana* Vaughan, 1919, paratype, USNM 325082, USGS locality 6775, White Springs, Florida
6. *Goniopora imperatoris* Vaughan, 1919, holotype, USNM 325049, USGS locality 6016, Empire Quarry, Canal Zone
7. *Goniopora canalis* Vaughan, 1919, original syntype designated as lectotype herein, USNM 72891, USGS locality 6016, Empire Quarry, Canal Zone
8. *Goniopora tampaensis* Weisbord, 1973, holotype, USNM 68317, USGS locality 2084, Tampa, Florida

(2) *Septal structure and arrangement.*—The septa are composed of vertical trabeculae joined by horizontal septal junctions and synapticulae. These junctions outline the pores, diagnostic of the poritids. A granule (herein termed "denticle") is formed on the surface of each trabecula. Two types of measures describe the vertical trabeculae: (a) number of denticles per septum (**DS**), a measure which can be used to estimate number of trabeculae per septum and (b) septum thickness (**T1**, **T2**, **T3**), which can be used to estimate the size of respective trabeculae. Similarly, two types of measures describe the synapticulae: (a) number of synapticular rings (**SR**), and (b) synapticula thickness (**SY**).

The septa are bilaterally arranged in a diagnostic formula described in detail by Bernard (1903, 1905). They are commonly termed "dorsal" (one directive septum), "ventral" (a septal triplet), and "lateral" (four septal pairs) in *Porites*, and "primary" (one cycle of six directive septa), "secondary" (one cycle of six septa), and "tertiary" (one cycle of twelve minor septa) in *Goniopora* (see Text-fig. 8 for orientation). The total number of septa per calice (**NS**) was first counted, and the pattern of septal fusion was noted (**F1**, **F2** in *Goniopora*). The ventral triplet was almost always fused in *Porites* and rarely free. A trident (*sensu* Bernard, 1905) was never seen. The lengths of each type of septum (**L1**, **L2**, **L3**) were measured in both genera, and any apparent "bifurcations" near the wall (**NB**) were noted. In the material studied, such bifurcations were usually caused by decreased calcification rather than by actual forking of trabecular rows. They therefore do not represent incipient septa.

(3) *Development of the pali.*—The pali are not true "pali" [defined in Vaughan and Wells (1943) and Wells (1956) as separate, discrete structures formed by septal substitution], but are similar to paliform lobes, formed by development of the innermost septal trabeculae



Text-figure 8.—Drawings showing some of the characters measured. (A) *Porites*: corallite diameter, **CD**; dorsal septum length, **L1**; ventral septum length, **L2**; lateral septum length, **L3**; ventral palus thickness, **P2**; columella tubercle length, **C1**; columellar synapticular ring diameter, **CW**; wall thickness, **WT**. (B) *Goniopora*: corallite diameter, **CD**; primary septum length, **L1**; secondary septum length, **L2**; tertiary septum length, **L3**; secondary palus thickness, **P2**; columella tubercle length, **C1**; columella tangle width, **CW**; wall thickness, **WT**.

Table 2.—List of Neogene Mediterranean poritid types and modern Caribbean specimens used in statistical analyses.

Neogene Mediterranean:

1. *Porites collegniana* Michelin, 1842, figured specimen in Chevalier (1961), MHNP #P-324-C, Mérignac, Aquitaine, France
2. *Porites incrustans* Milne-Edwards and Haime, 1851, figured specimen in Reuss (1872) NHMW 1859-XLV-649b, Forchtenau, Hungary
3. *Porites maigensis* Kühn, 1925, holotype, Eggenburg Museum, Maïgen near Eggenburg, Austria
4. *Porites pachysepta* Chevalier, 1961, holotype, MHNP, Villandraut, Aquitaine, France
5. *Porites mancietensis* Chevalier, 1961, holotype, MHNP, Manciet, Aquitaine, France
6. *Porites lobatosepta* Chevalier, 1961, holotype, MHNP, Popogna, Livorno, Italy
7. *Porites calabricae* Chevalier, 1961, holotype, MHNP, Vibo Valentia, Calabria, Italy
8. *Porites leptoclada* Reuss, 1872, holotype, NHMW 1872-XIII-80, Niederleis near Enzefeld, Austria
9. *Goniopora globulosa* Chevalier, 1961, holotype, MHNP, St. Paul-Les-Dax, Aquitaine, France
10. *Goniopora granosa* Chevalier, 1961, holotype, MHNP, Peyrère de Peyrehorade, Aquitaine, France
11. *Goniopora turonensis* Chevalier, 1961, holotype, MHNP, Pontlevoy, Touraine, France

Modern Caribbean:

1. *Porites astreoides* Lamarck, 1816, holotype, MHNP, Lamarck Collection #149, Mers d'Amérique
2. *Porites astreoides* Lamarck, 1816, USNM 15521, Dry Tortugas

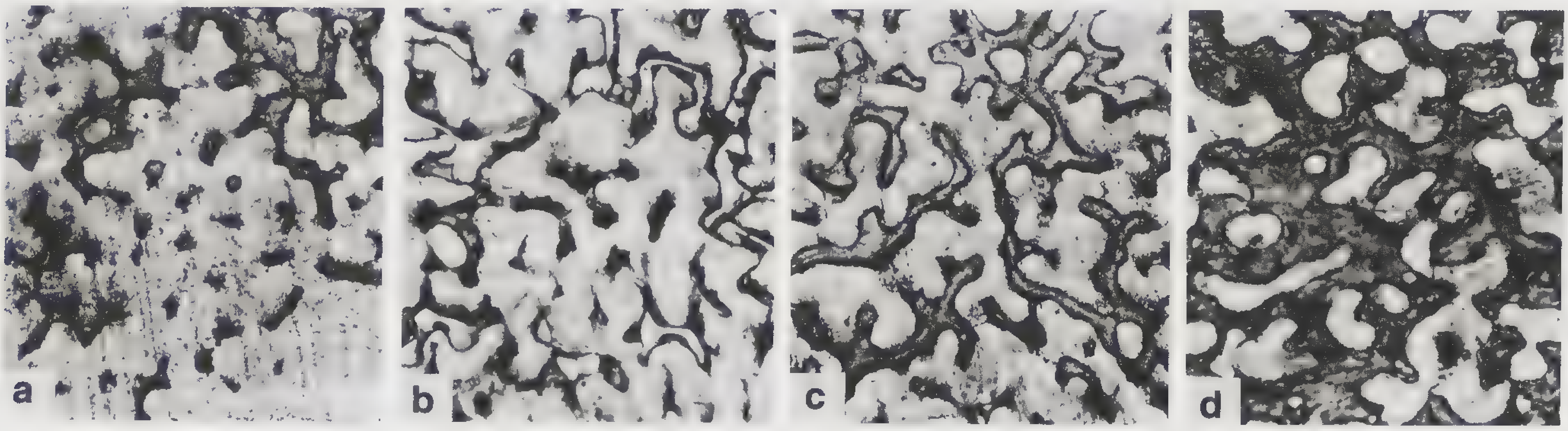
3–4. *Porites astreoides* Lamarck, 1816, YPM 7077–7078, Laborel Collection, Recife Military Air Base, Brazil

5. *Porites astreoides braziliensis* Verrill, 1901a, holotype, YPM 4539, Maria, Farinha, Pernambuco, Brazil
6. *Porites porites* (Pallas, 1766), Senckenburg Museum, Esper Collection #19, locality unknown
7. *Porites porites* (Pallas, 1766), USNM 72375, Florida Keys, locality C-12
8. *Porites clavaria* Lamarck, 1816, holotype, MHNP, Lamarck Collection #150, Antilles
9. *Porites clavaria* Lamarck, 1816, USNM 15860, Dry Tortugas
10. *Porites furcata* Lamarck, 1816, holotype, MHNP, Lamarck Collection #154, Mers d'Amérique
11. *Porites furcata* var. 2 of Lamarck, 1816, MHNP, Lamarck Collection #155, Mers d'Amérique
12. *Porites furcata* Lamarck, 1816, USNM 15860, Dry Tortugas
13. *Porites divaricata* Lesueur, 1821, USNM 72377, locality C-45, east of Pulaski Bay, Florida
14. *Porites branneri* Rathbun, 1887, holotype, USNM 10961, Parahyba do Norte, Brazil
15. *Porites branneri* Rathbun, 1887, paratype, USNM 10962, Canderas Reef, Pernambuco, Brazil
16. *Porites branneri* Rathbun, 1887, YPM 9079, Laborel Collection, Abrolhos Archipelago, Brazil
17. *Porites branneri* Rathbun, 1887, YPM 9080, Laborel Collection, Fernando de Novonha Is., Brazil
18. *Porites verrilli* Rehberg, 1893, holotype, YPM 4539, Albrolhos Reefs, Brazil

(Text-fig. 9). For consistency with other previous poritid studies, the term "palus" is nevertheless retained. The number of pali (**PL**) was counted within each calice, and the widths of those corresponding to the three septal types (**P1**, **P2**, **P3**) measured. A synapticular ring connecting all pali within each calice was often found in *Porites* and the distance across this ring (**CW**) was measured.

(4) *Size and structure of the columella tubercle.*—In *Porites,* the columella consists of an isolated tubercle aligned parallel to the dorsoventral axis and supported by the columellar synapticular ring connecting the pali. In *Goniopora,* the columella consists of a tangle of twisted trabeculae extending from the inner margins of the septa. In *Porites,* the length (**C1**) and the width (**C2**) of the tubercle were measured. In *Goniopora,* the length (**C1**) and the width (**C2**) of an upper lobe of a central trabecula (termed "tubercle") were measured, as well as the width of the entire columella tangle (**CW**).

(5) *Size and structure of the coenosteal reticulum.*—



Text-figure 9.—Serial acetate peels down one corallite of *Porites furcata.* (A), (B), and (C) were made at regular 0.1-mm intervals from the colony surface, and (D) was made 0.3 mm below (C). In (A), six pali are clearly seen surrounding a thin columella tubercle. In (B), the pali are five in number and begin to blend with the septa. The dorsal palus has already merged. In (C), the pali are no longer visible and the corallite outline begins to disappear into an irregular (faintly radial) meshwork of septal trabeculae. In (D), the corallite has disappeared altogether, and the skeletal meshwork appears structureless and more heavily calcified.

As described in detail by Bernard (1905), the wall or theca consists of one or more rows of vertical trabeculae united by synapticulae. When more than one row is involved, the trabecular complex is usually termed "wall reticulum" or even "coenosteal reticulum". The reticulum is not true coenosteum, however, but is formed by addition of discrete rows of intervening mural trabeculae and not by accretion or deposition of structurally-different skeletal material. This coenosteal reticulum is the only skeletal material that separates corallites. It may form bulges or ridges across the calical surface. Three measures describe the amount of coenosteal reticulum separating calices: corallite spacing (**CS**), number of rows of mural trabeculae (**WR**), and wall thickness (**WT**). One additional measure (total number of mural denticles, **DW**) describes the overall texture of this reticulum.

STATISTICAL PROCEDURES

Species were distinguished within each of the two common genera, *Porites* and *Goniopora,* using multivariate statistical analyses similar to those outlined in Foster (1984). First, the means for each colony in the NMB collections were assigned to preliminary groups within each genus using cluster analysis (BMDP program 2M, Dixon, 1981). All measured characters were used in the analyses. Eight groups were formed in *Porites* and four in *Goniopora.*

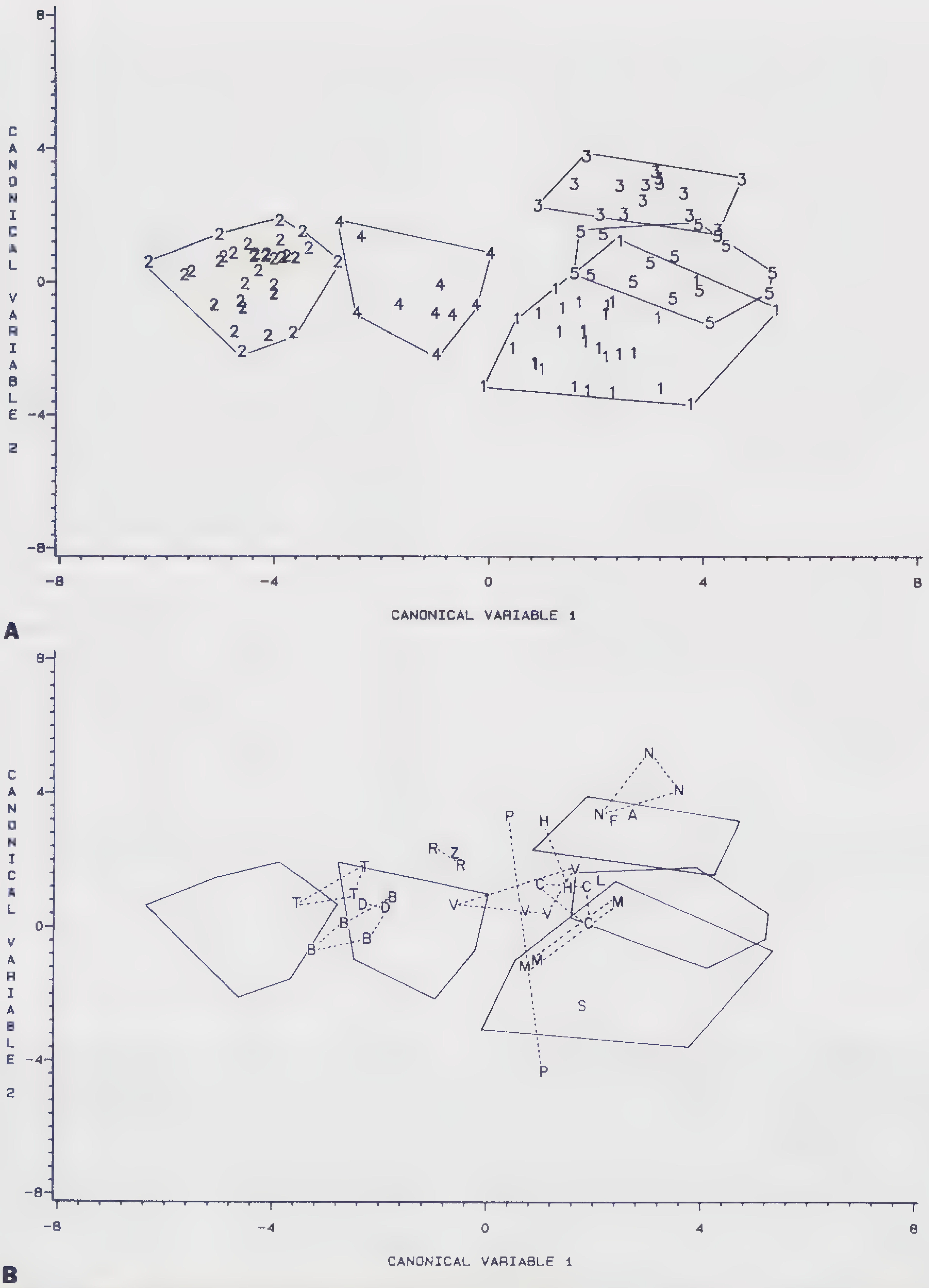
Next, these groups were re-analyzed using a series of stepwise discriminant analyses (BMDP program 7M, Dixon, 1981). In this process, analyses were also run using data for individual corallites, and group assignments for colonies were changed so that all corallites within each colony belonged to the same group. In cases showing extensive overlap between groups, the overlapping groups were analyzed separately. If the groups still showed considerable overlap, the groups were combined and then re-evaluated together with all groups within the genus. Group assignments for colonies lying at cluster margins were further modified by trial and error to obtain the highest percentage of correctly-classified corallites. Because of poor preservation of some of the type specimens, a few characters (primarily related to thickness) were dropped from the final analyses. All measured characters except **DS**, **SR**, **SD**, and **SY** were used in the final *Porites* analysis. All characters except **F1**, **F2**, **DS**, **T1**, **T2**, **T3**, **SD**, and **SY** were used in the final *Goniopora* analysis. The final results yielded five groups among the NMB specimens in *Porites* (Text-fig. 10a) and three in *Goniopora* (Text-fig. 11a). These groups represent the species described in this study.

Finally, using the NMB species groups and adding the measured types from Table 1, two further discriminant analyses (BMDP program 7M, Dixon, 1981) were performed: (1) the analyses were rerun leaving the types unclassified, (2) the analyses were rerun so that each NMB group and group of types were classified separately. The results (Text-figs. 10b, 11b) revealed a very complicated relationship between the types and the

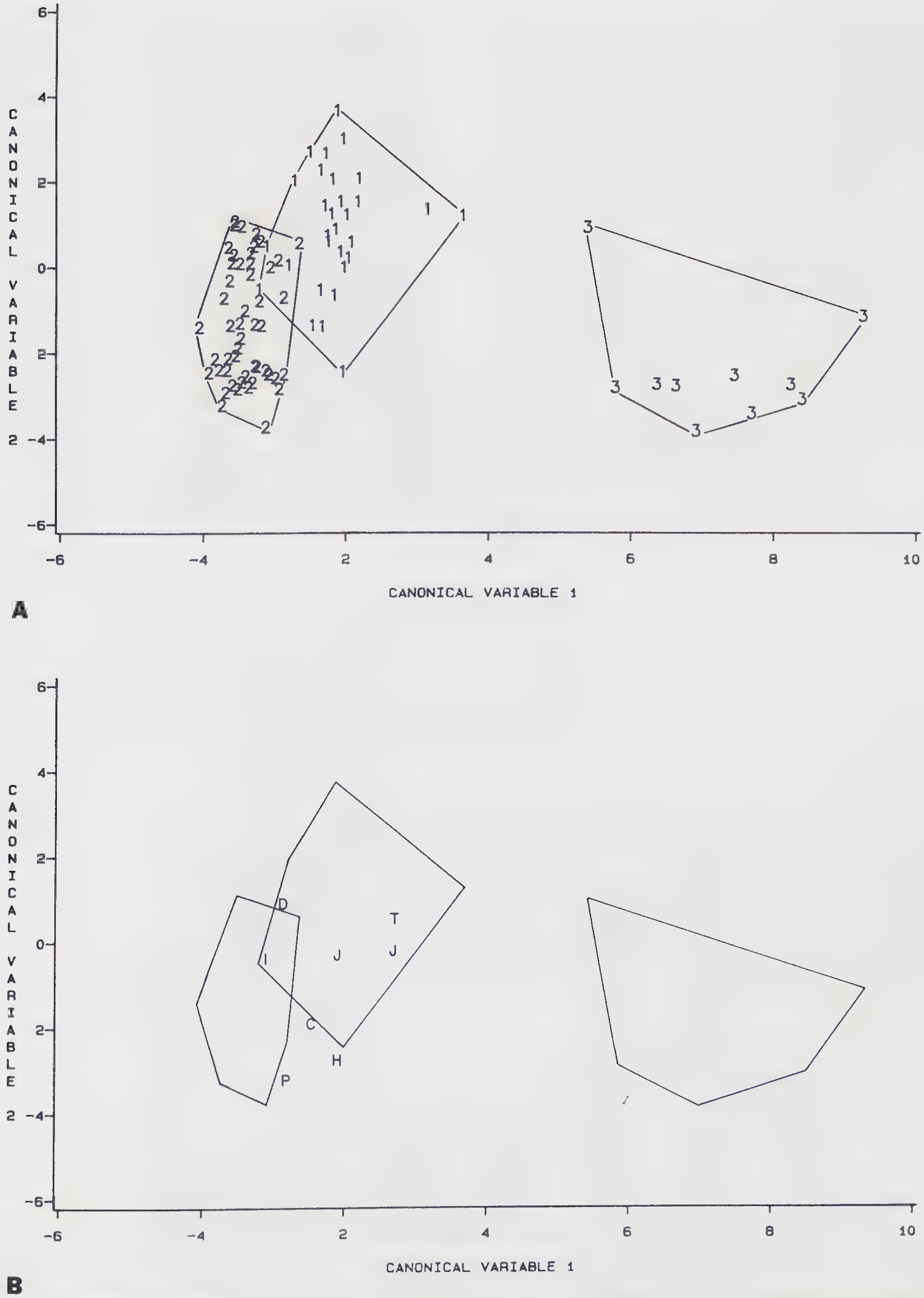
Table 5.—Weighting of characters in the all *Porites* canonical discriminant analysis. Total-sample correlations between the canonical variables and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. The four canonical variables are labelled CV1–4. Abbreviations for characters are explained in Table 3.

Original variable	CV1		CV2		CV3		CV4	
	COR	SCC	COR	SCC	COR	SCC	COR	SCC
CD	—	0.87	−0.422	—	—	−0.51	−0.340	—
CS	0.764	—	—	−1.01	0.288	1.10*	—	0.81
L1	—	—	−0.610*	−1.19	—	—	—	—
L2	—	—	−0.492	—	—	0.71	—	—
L3	—	—	−0.574	—	—	—	—	0.58
NN	—	—	—	—	—	—	0.467	0.73
NB	−0.616	—	—	—	0.263	0.54	—	—
DW	−0.538	—	−0.457	—	—	—	—	—
PL	−0.522	—	—	—	—	−0.65	—	—
WR	0.900*	1.47*	—	−1.75*	—	—	—	—
T1	—	—	—	—	—	—	−0.487	—
T2	—	—	—	—	0.316	0.84	−0.536*	—
T3	—	—	—	—	—	—	−0.458	—
P2	−0.530	—	—	—	—	—	—	
C1	0.648	—	—	—	—	−0.43	—	—
C2	0.578	—	—	—	—	−0.50	—	—
CW	0.667	—	—	0.96	0.264	—	−0.474	−1.50*
WT	0.905*	—	—	1.90*	—	—	—	—
SE	—	−0.72	—	—	−0.577*	−0.65	—	−0.75
WE	0.607	0.89	—	—	−0.517*	−0.69	—	0.92

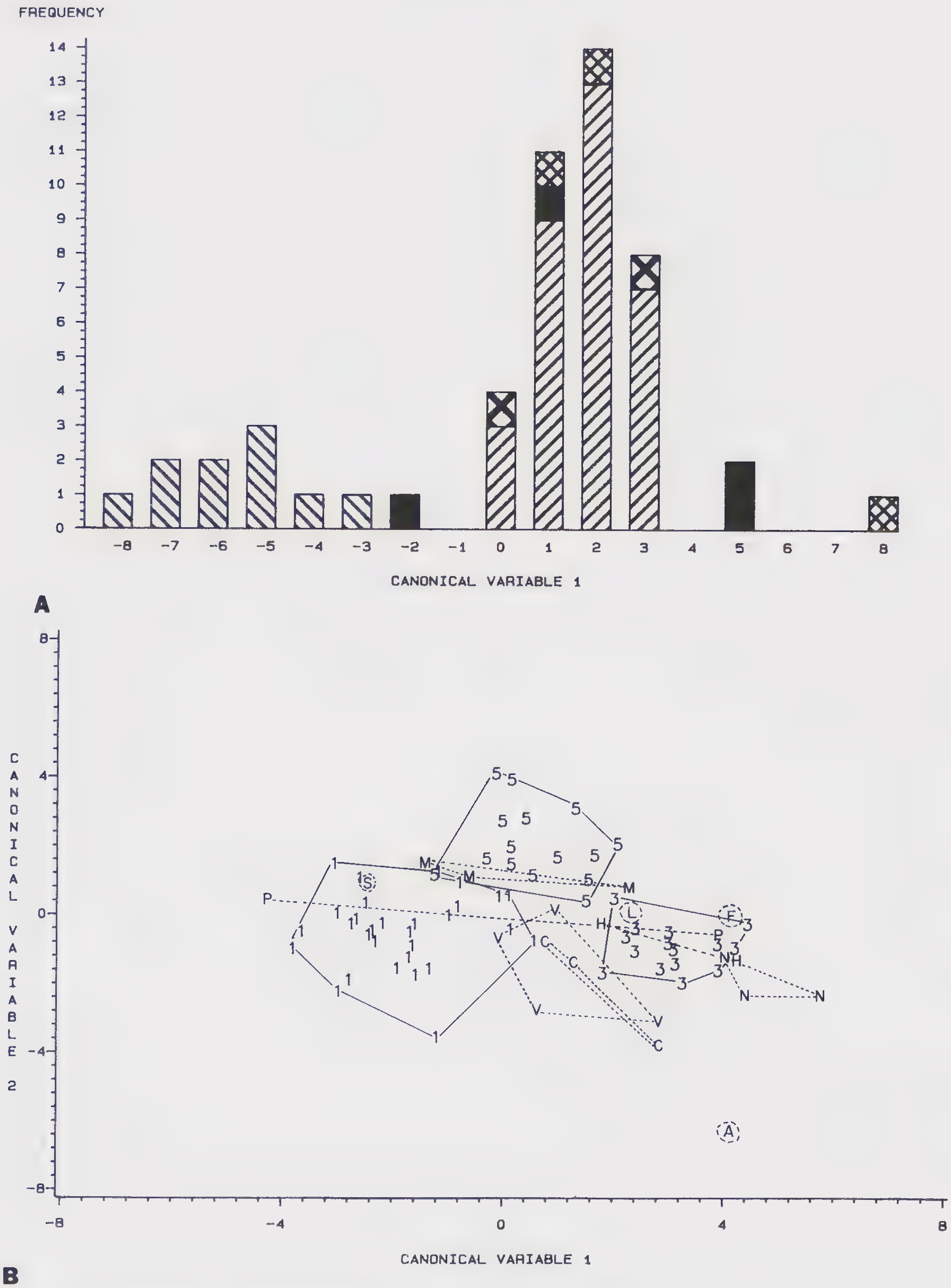
* most important variables.



Text-figure 10.—*Porites.* Canonical discriminant analysis of the NMB collections. (A) Plot of scores on the first two canonical variables showing polygons outlining the range of variation between colonies in the five species groups defined by the statistical analyses. The points represent means for each colony. 1 = *P. portoricensis,* 2 = *P. baracoaensis,* 3 = *P. waylandi,* 4 = *P. convivatoris,* 5 = *P. macdonaldi.* (B) Plot of scores showing polygons around the NMB species groups [as given in (A)] and points representing the colony means of the measured types. A = type 23, B = types 12–14, C = types 9–11, D = types 15–16, F = type 30, H = types 24–25, L = type 31, M = types 26–28, N = types 20–22, P = types 2–3, R = type 29, S = type 32, T = types 17–19, V = types 4–8, Z = type 1. The numbers for types refer to specimens listed in Table 1.



Text-figure 11.—*Goniopora.* Canonical discriminant analysis of the NMB collections. (A) Plot of scores on the first two canonical variables showing polygons outlining the range of variation between colonies in the three species groups defined by the statistical analyses. The points represent individual corallites. 1 = *G. hilli,* 2 = *G. imperatoris,* 3 = *G. calhounensis.* (B) Plot of scores showing polygons around the NMB species groups [as given in (A)] and points representing the colony means of the measured types. C = type 7, D = type 3, H = type 1, I = type 6, J = types 4–5, P = type 2, T = type 8. The numbers for types refer to specimens listed in Table 1.



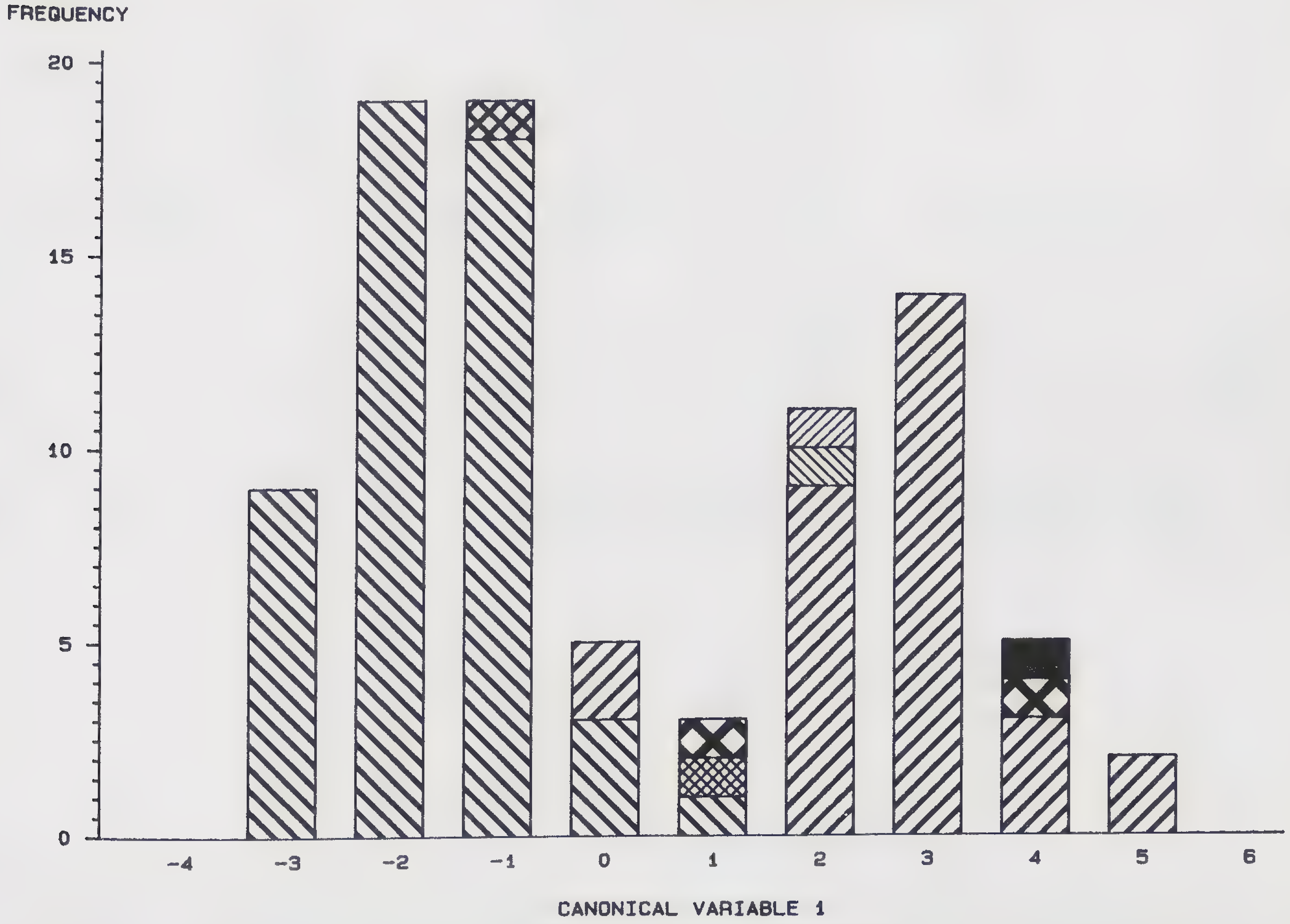
Text-figure 12.—*Porites* subgroups. Canonical discriminant analysis of the NMB collections. (A) Groups 2 and 4, *P. baracoaensis* and *P. convivatoris.* Histogram giving frequencies of colony means for scores on the canonical variable. Left angle stripes = NMB *P. baracoaensis*; right angle stripes = NMB *P. convivatoris*; solid = types 12–14; small crosshatch = types 17–19; large crosshatch = types 15–16. The numbers for types refer to specimens listed in Table 1. (B) Groups 1, 3, and 5; *P. portoricensis, P. waylandi,* and *P. macdonaldi.* Plot of scores on the first two canonical variables showing polygons outlining the range of variation between colonies in the NMB species groups. The points represent means for each colony. 1 = NMB *P. portoricensis,* 3 = NMB *P. waylandi,* 5 = *P. macdonaldi,* A = type 23, C = types 9–11, F = type 30, H = types 24–25, L = type 31, M = types 26–28, N = types 20–22, P = types 2–3, S = type 32, V = types 4–8. The numbers for types refer to specimens listed in Table 1.

NMB species groups. To interpret this relationship, the *Porites* were divided into two subsets, the first composed of NMB species groups 2 (*P. baracoaensis* Vaughan, 1919) and 4 (*P. convivatoris,* n. sp.) and the second encompassing NMB species groups 1 [*P. portoricensis* (Vaughan, 1919)], 3 (*P. waylandi,* nom. nov.), and 5 (*P. macdonaldi* Vaughan, 1919). Each subset was reanalyzed together with only those types that originally lay near the constituent NMB species groups. The results are shown in Text-figure 12. Similarly in *Goniopora,* NMB species groups 1 (*G. hilli* Vaughan, 1919) and 2 (*G. imperatoris* Vaughan, 1919) have been reanalyzed alone with all the *Goniopora* types (Text-fig. 13). These analyses form the basis of: (1) the synonymies and the distribution patterns given in the formal systematic descriptions and (2) the brief discussions given on biostratigraphy and paleoecology. The results shown on Text-figures 10 through 13, Tables 5 and 6, and Appendix IIa–d are based on the results of the SAS CANDISC procedure (SAS Institute, 1982) run at the

Table 6.—Weighting of characters in the all *Goniopora* canonical discriminant analysis. Total-sample correlations between the canonical variables and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. The canonical variables are labelled CV1–2. Abbreviations for characters are explained in Table 4.

Original variable	CV1		CV2	
	COR	SCC	COR	SCC
CD	0.918*	1.04*	—	—
CS	0.838	0.54	—	—
L1	0.887*	—	—	−0.90*
L2	0.907*	—	—	0.93*
L3	0.910*	0.91*	—	—
DW	0.657	—	—	—
PL	—	—	−0.510*	−0.59
SR	0.520	—	0.349	0.65
P2	—	—	−0.312	—
C2	0.548	0.58	—	0.47
CW	0.633	—	−0.332	—
SY	0.652	0.50	−0.366	—
WT	0.596	—	−0.339	−0.64
SE	—	—	0.452	0.72

* most important variables.



Text-figure 13.—*Goniopora* subgroup. Canonical discriminant analysis of the NMB collections. Histogram giving frequencies of colony means of scores on the canonical variable. Left angle stripes = NMB *G. imperatoris*; right angle stripes = NMB *G. hilli*; small left angle stripes = type 7; small right angle stripes = type 1; solid = type 8; small crosshatch = type 3; medium crosshatch = type 6; large crosshatch = types 4–5. The numbers for types refer to specimens listed in Table 1.

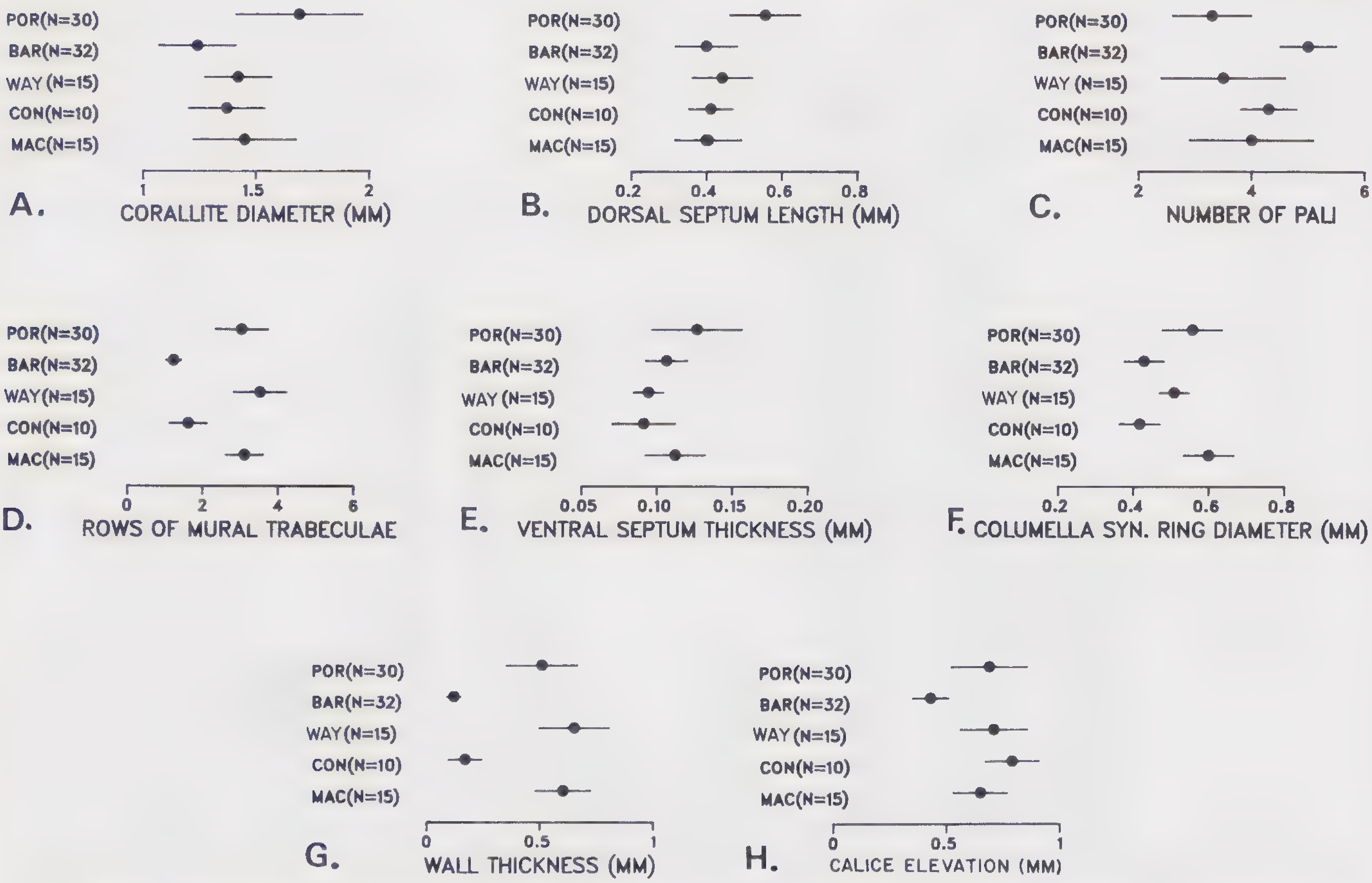
University of Iowa. In all Text-figures, Tables, and Appendices, the data used in *Porites* represent colony means, whereas in *Goniopora,* they represent individual corallites.

Means and standard deviations of all single characters are given for each species in Appendix Ia, b. Eight characters revealing highly-significant differences between species are plotted for *Porites* in Text-figure 14 and for *Goniopora* in Text-figure 15. Intraspecific variation was found to be roughly equivalent in the calculated canonical variables for all species in each genus using Box's test (Miller, 1968).

RESULTS AND INTERPRETATIONS

As described in the previous section, five separate canonical discriminant analyses were performed to distinguish species and relate them to type material: (1) all five groups of *Porites,* (2) groups 2 and 4 of *Porites,* (3) groups 1, 3, and 5 of *Porites,* (4) all three groups of *Goniopora,* and (5) groups 1 and 2 of *Goniopora.* The results of each analysis are as follows:

(1) All five groups of *Porites*: 1, *P. portoricensis*; 2, *P. baracoaensis*; 3, *P. waylandi*; 4, *P. convivatoris*; 5, *P. macdonaldi.*—Five groups were distinguished in this analysis, with 90.2 percent of all colonies classified correctly (Text-fig. 10a). 80 percent were correctly classified in groups 1 and 4, 93.3 percent in groups 3 and 5, and 100 percent in group 2. Four canonical variables (CV1–CV4) were calculated, with CV1 accounting for 77.7 percent of the variation, CV2 for 11.4 percent, CV3 for 6.7 percent, and CV4 for 4.2 percent. The initial stepwise analysis (computed using the program BMDP-7M) showed that the groups could be distinguished using a minimum of seven characters (in decreasing importance: **WE**, **L1**, **CW**, **NB**, **WR**, **NN**, and **SE**). However, 20 of the 25 measured characters were important in computing the character combinations that best distinguished the five species in the total canonical analysis (computed using the SAS CANDISC procedure) (Table 5). The first canonical variable (CV1) distinguished three major groups: group 2, group 4, and a combination of groups 1, 3, and 5. It weighted

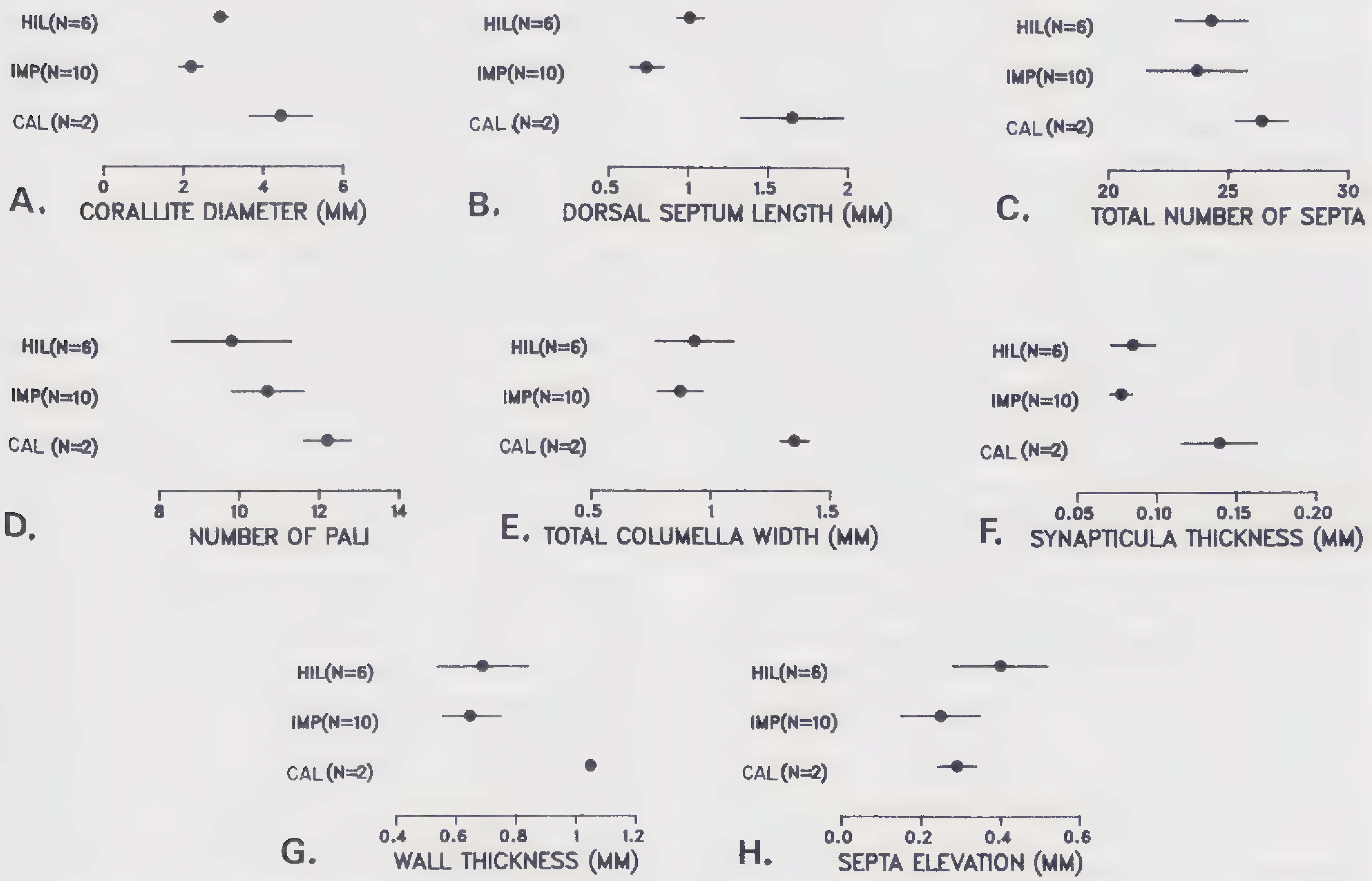


Text-figure 14.—Means and standard deviations for eight characters in the five *Porites* species. The midpoint of each horizontal line represents the mean, and the length of the line on either side of the midpoint is one standard deviation. Analysis of variance (or Welch's statistic when variances are unequal) shows that the species are significantly different in each case. Levene's test for equal variances shows that variances are equal only in dorsal septum length. POR = species 1, *P. portoricensis*; BAR = species 2, *P. baracoaensis*; WAY = species 3, *P. waylandi*; CON = species 4, *P. convivatoris*; MAC = species 5, *P. macdonaldi.* "N" = number of colonies measured. (A) corallite diameter, **CD**, (B) dorsal septum length, **L1**, (C) number of pali, **PL**, (D) number of rows of mural trabeculae, **WR**, (E) ventral septum thickness, **T2**, (F) columellar synapticular ring diameter, **CW**, (G) wall thickness, **WT**, (H) total calice elevation, **WE**.

number of rows of mural trabeculae (**WR**) most heavily and is strongly correlated with the number of rows of mural trabeculae (**WR**) and wall thickness (**WT**). The second canonical variable (CV2) distinguished between groups 1, 3, and 5. It again weighted the number of rows of mural trabeculae (**WR**) heavily but is best correlated with the inverse of the lengths of the three septal types (**L1**, **L2**, **L3**). Various characters are heavily weighted on canonical variables 3 and 4 (CV3, CV4), with corallite spacing (**CS**) most important in CV3 and total columella width (**CW**) most important in CV4. Two measures of calice elevation (**SE**, **WE**) are inversely correlated with CV3, and septal thickness (**T1**, **T2**) is inversely correlated with CV4.

(2) Groups 2 (*P. baracoaensis*) and 4 (*P. convivatoris*) of *Porites*.—Two groups were distinguished in this analysis, with 100 percent of all colonies correctly classified (Text-fig. 12a). The canonical variable calculated explained 100 percent of the variation. Nine of the 25 characters were important in the total canonical analysis (Appendix IIa). Columella tubercle length (**C1**) was most heavily weighted in the canonical variable, and calice elevation (**WE**) is most strongly correlated. The canonical variable appears most similar to CV3 of the first analysis. Study of the position of the types on the histogram for the canonical variable shows that types for three described species belong to group 2, whereas no types belong to group 4.

(3) Groups 1 (*P. portoricensis*), 3 (*P. waylandi*), and 5 (*P. macdonaldi*) of *Porites*.—Three groups were distinguished in this analysis, with 85 percent of all colonies classified correctly (Text-fig. 12b). 85.7 percent were correctly classified in groups 3 and 5, and 83.3 percent in group 1. Two canonical variables were calculated, which explained 74.7 percent and 25.3 percent of the variation respectively. Fifteen of the 25 characters were important in the total canonical analysis (Appendix IIb). Septum length (**L1**) was most heavily weighted and most strongly correlated on the first canonical variable (CV1), which appears most similar to



Text-figure 15.—Means and standard deviations for eight characters in the three *Goniopora* species. The midpoint of each horizontal line represents the mean, and the length of the line on either side of the midpoint is one standard deviation. Analysis of variance (or Welch's statistic when variances are unequal) shows that the species are significantly different in each case. Levene's test for equal variances shows that variances are unequal only in corallite diameter, dorsal septum length, and synapticula thickness. HIL = species 1, *G. hilli*; IMP = species 2, *G. imperatoris*; CAL = species 3, *G. calhounensis*. "N" = number of colonies measured. (A) corallite diameter, **CD**, (B) primary septum length, **L1**, (C) total number of septa, **NS**, (D) number of pali, **PL**, (E) columella tangle thickness, **CW**, (F) synapticula thickness, **SY**, (G) wall thickness, **WT**, (H) septa elevation, **SE**.

CV2 in the first analysis. Total columella width (**CW**) was most heavily weighted on CV2, which is best correlated with the number of neighboring corallites (**NN**), the inverse of septum thickness (**T2**), and the inverse of total columella width (**CW**). CV2 appears most similar to CV4 of the first analysis. Study of the distances of types from these three group centroids shows that: (1) two described species belong to group 1, (2) four described species belong to group 3, (3) one described species belongs to group 5, and (4) the positions of two described species lie intermediately between groups 1 and 3. Further subjective examination of variation in overall colony shape within these three species shows that the two intermediate described species most likely belong to group 1. This information together with the poor preservation of types for the two additional described species that initially appeared to belong to group 3 suggests that they may instead belong to group 1.

(4) All three groups of *Goniopora*: 1, *G. hilli*; 2, *G. imperatoris*; 3, *G. calhounensis*.—Three groups were distinguished in this analysis, with 91.1 percent of all corallites correctly classified (Text-fig. 11a). 92 percent were correctly classified in group 2, and 90 percent were correctly classified in groups 1 and 3. Two canonical variables (CV1, CV2) were calculated, with the first accounting for 93.6 percent of the variation and the second for only 6.4 percent. The stepwise discriminant analysis showed that only four (in descending order: **CD**, **L3**, **PL**, **SR**) of the 21 characters were needed to distinguish between the three groups. However, in the total canonical analysis, 14 of the 21 measured characters were important (Table 6). The first canonical variable (CV1) distinguished the three groups, although overlap between groups 1 and 2 still persisted. It weighted corallite diameter (**CD**) and tertiary septum length (**L3**) most heavily and is very strongly correlated with corallite diameter (**CD**) and septum length (**L1**, **L2**, **L3**). The second canonical variable (CV2) primarily distinguished groups 1 and 2. It also weighted septum length (**L1**, **L2**) most heavily but is inversely correlated with number of pali (**PL**). Study of the distances of the types from these three group centroids (Text-fig. 11b) shows that no types belong to group 3, and types for seven described species lie near groups 1 and 2.

(5) Groups 1 (*G. hilli*) and 2 (*G. imperatoris*) of *Goniopora*.—Two groups were distinguished in the analysis, with 95 percent of all corallites correctly classified (Text-fig. 13). 93.3 percent were correctly classified in group 1, and 96.0 percent in group 2. The one canonical variable calculated explained 100 percent of the variation. Nine of the 21 characters were important in the total canonical analysis (Appendix IIc). Corallite diameter (**CD**) was most heavily weighted and strongly correlated with the canonical variable. Study of the position of the types on the histogram calculated for the canonical variable shows that types for four described species belong to group 1, the type of one described species belongs to group 2, and the type for one described species is intermediate between groups 1 and 2. One additional canonical discriminant analysis was performed classifying three Dominican Republic groups and all seven described species as 10 separate groups. The results of the analysis clearly indicated that the intermediate belonged to group 2.

In summary, the results for *Porites* show that:

(1) Five slightly overlapping groups exist. The most overlap occurs in the species having an extensive coenosteal reticulum. The overlap is greater than that found in early Miocene species of *Montastraea* Blainville, 1830 (see Foster, 1984).

(2) Almost all the measured characters are important for distinguishing the five groups in the analysis. Four major character complexes were involved in this distinction: (a) development of the wall reticulum; (b) corallite size; (c) calice elevation; and (d) septal and columellar thickness. The pali do not appear to play as important a role in species discrimination as they do in modern Pacific poritids (see Veron and Pichon, 1982).

(3) Analyses of type material for 15 described species show that three described species belong to group 2 (*P. baracoaensis*), possibly six to group 1 (*P. portoricensis*), two to group 3 (*P. waylandi*), and one to group 5 (*P. macdonaldi*). This results in the total synonymization of eight described species with four previously described species.

(4) One new species (group 4, *P. convivatoris*) is recognized.

In summary, the results for *Goniopora* show that:

(1) Three groups exist. The two more abundant groups overlap slightly.

(2) Two-thirds of the measured characters are important in distinguishing the groups. Two major character complexes were involved in this distinction: (a) corallite size; and (b) number of pali (and to a lesser degree, calice elevation).

(3) Analyses of type material for seven previously described species show that four described species belong to group 1 (*G. hilli*), two to group 2 (*G. imperatoris*), and none to group 3 (*G. calhounensis*). At the end of the project, however, one type was found that could subjectively be assigned to group 3. This results in the total synonymization of five species with three previously-recognized species.

GENERAL COMPARISONS WITH OTHER FAUNAS

The results have been statistically compared with

two separate faunas to obtain further information on the spatial and temporal distribution of each species cluster. These two faunas are: (1) the Miocene Mediterranean poritids described by Chevalier (1961) and (2) described species of modern Caribbean poritids. The material studied is listed in Table 2.

(1) *Miocene Mediterranean poritids.*—Frost (1977c) has suggested that greater than 50 percent of the Caribbean reef-coral species in the Oligocene also occurred in the Mediterranean region. This overlap occurs especially in the suborder Faviina of the classification system of Vaughan and Wells (1943), a suborder different from the one under consideration (*i.e.,* the family Poritidae belongs to the suborder Fungiina); however, Frost does report high similarities between three Oligocene species of *Goniopora* and one Oligocene species of *Alveopora* in the two regions. In contrast, little overlap is reported between species of *Porites.* No such general comparisons have been made between Caribbean and Mediterranean reef-corals for the Miocene. In the present study, types of 11 Miocene Mediterranean poritid species (three of the five specimens of *Goniopora* and all eight specimens of *Porites*) described by Chevalier (1961) (Table 2) were measured, and their canonical scores were calculated using the canonical variables of the analyses of the five species of *Porites* and three species of *Goniopora* described in the previous section. The results are given in Text-figure 16.

In *Porites* (Text-fig. 16a), the Mediterranean species appear different from the Caribbean species. Only one species, *P. maigensis* Kühn, 1925, has a high CV1 value signifying a well-developed wall reticulum, which is characteristic of Dominican Republic groups 1, 3, and 5 (*P. portoricensis, P. waylandi,* and *P. macdonaldi,* respectively). Similarly, all eight Mediterranean species have high values for CV2 indicating small-sized calices. One Mediterranean species, *P. mancietensis* Chevalier, 1961, is shown to fall within the species 2 polygon (*P. baracoaensis*), and three Mediterranean species, *P. lobatosepta* Chevalier, 1961, *P. incrustans* Milne-Edwards and Haime, 1851, *P. leptoclada* Reuss, 1872, fall within the species 4 polygon (*P. convivatoris*). Further study of colony shape (see "Comparison" sections following under *Systematic Paleontology*), however, indicates that the Caribbean and Mediterranean species are not synonymous.

In *Goniopora* (Text-fig. 16b), only one Mediterranean species appears similar to any Caribbean species (*i.e.,* species 1, *G. hilli*). The corallite diameters of the remaining four species described by Chevalier (1961) are considerably larger than the Caribbean material. The one similar Mediterranean species (*G. turonensis* Chevalier, 1961), however, again has a distinctly different colony shape; therefore, the Caribbean and Mediterranean species are probably not synonymous.

In summary, these analyses suggest that:

1. No *Porites* or *Goniopora* species probably cooccur in the Mediterranean and Caribbean regions during the Miocene.

2. The Mediterranean *Porites* generally have smaller corallites with less-developed wall reticula than the Caribbean *Porites.*

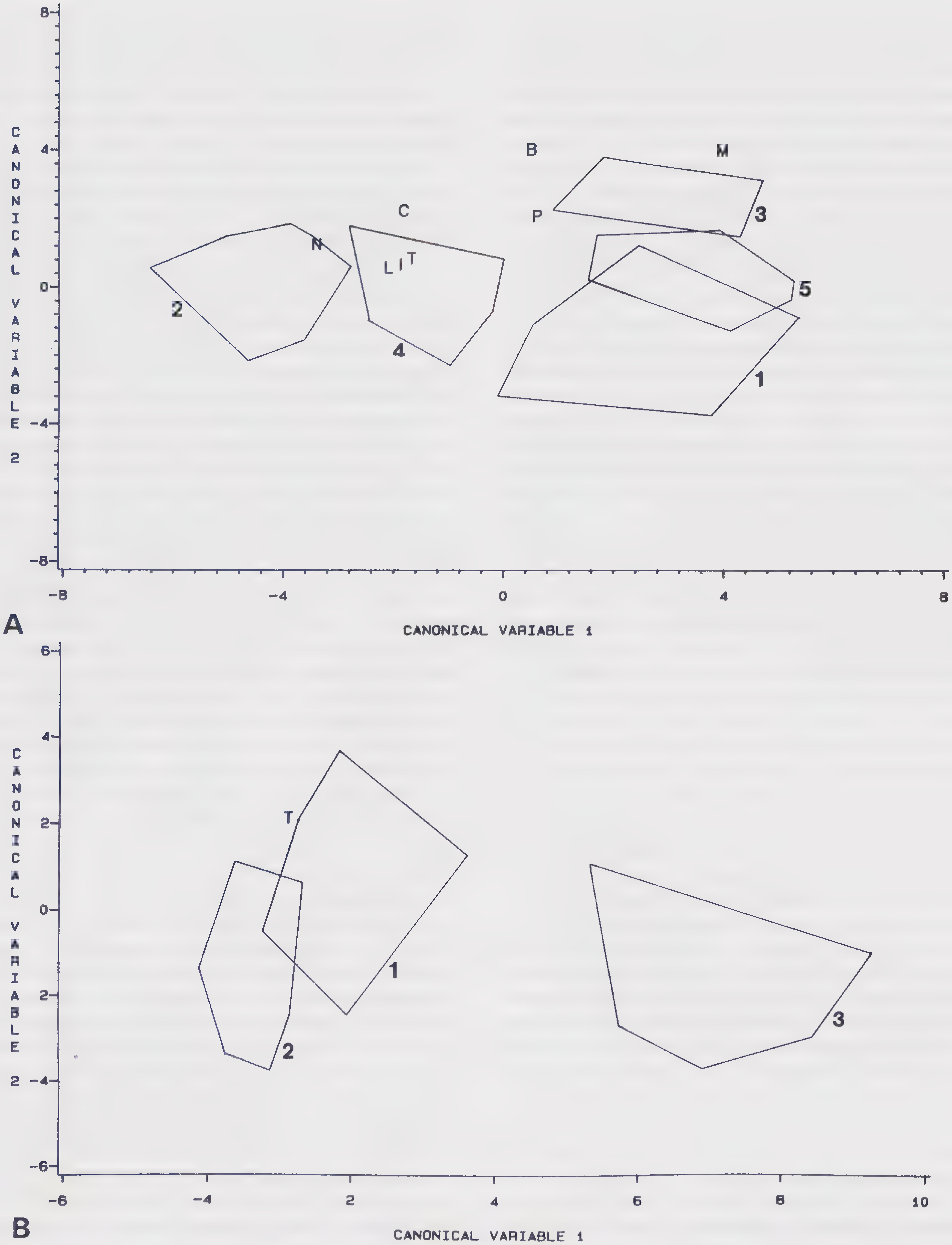
3. The Mediterranean *Goniopora* generally have larger corallites than the Caribbean *Goniopora.*

The differences between the Caribbean and Mediterranean poritids are more likely historical than adaptive in origin, since the two genera probably assumed similar ecologic roles in the two regions.

(2) *Modern Caribbean poritids.*—Only one of the three genera in the present study, *Porites,* is represented in the modern Caribbean. Types of six described modern Caribbean species [assuming *P. porites* (Pallas, 1766) = *P. clavaria* Lamarck, 1816] and the five Dominican Republic species groups were analyzed by canonical discriminant analysis using a total of 11 groups. The results are shown on Text-figure 17, and relative loadings for characters are given in Appendix IId. 79.3 percent of the colonies were correctly classified in this analysis. Seven canonical variables were calculated and the first canonical variable (CV1) explains 58.1 percent of the variation, CV2 19.8 percent, CV3 10.6 percent, CV4 4.8 percent, CV5 4.4 percent, CV6 2.0 percent, and CV7 0.2 percent. Of the two variables shown in Text-figure 17, wall thickness and number of rows of mural trabeculae are most important in CV1, and calice size and the inverse of calice elevation are most important in CV2.

Three significant interpretations can be made from these results:

(1) Modern Caribbean *Porites* are distinctly different from the five Neogene Dominican Republic species groups. Overlap occurs *only* with the species 4 polygon, which represents *P. convivatoris,* n. sp., an unusual species that forms small ellipsoidal colonies with an axial tube. Therefore, during the late Pliocene or Pleistocene, all five of the Dominican Republic species must have become extinct, and the modern *Porites* radiated to replace them ecologically. This hypothesis is supported by the occurrence of four modern species of *Porites* in the upper Pliocene/lower Pleistocene Caloosahatchee Formation of Florida and the absence there of all Neogene poritid species described herein (Weisbord, 1974). This evolutionary pattern in the poritids contrasts with that observed in *Montastraea* (Foster, in preparation), in which the two modern species are both represented in the Neogene Dominican Republic material.



Text-figure 16.—Classification of Neogene Mediterranean types using the canonical discriminant analyses of the NMB collections. (A) *Porites.* Plot of scores showing polygons around the NMB species (as given in Text-fig. 10a) and points representing the colony means of measured types. B = type 7, C = type 1, I = type 2, M = type 3, N = type 5, P = type 4, T = type 8. The numbers for types refer to specimens listed in Table 2. (B) *Goniopora.* Plot of scores showing polygons around the NMB species (as given in Text-fig. 11a) and points representing the colony means of measured types. T = type 11. Types 9 and 10 lie off the graph. The numbers for types refer to specimens listed in Table 2.

(2) The modern species have intermediate to high values for CV1 indicating that their coenosteal reticulum is generally well-developed and similar to that in species 4 (*P. convivatoris*) and the species complex 1/3/5 (*P. portoricensis, P. waylandi,* and *P. macdonaldi,* respectively). The highest values for CV1 occur in modern specimens from Brazil.

(3) The modern Caribbean species have significantly low values for CV2 indicating that they have smaller, more elevated calices than the fossil forms. Since the fossil material is exquisitely preserved, these results could not be caused by preservation.

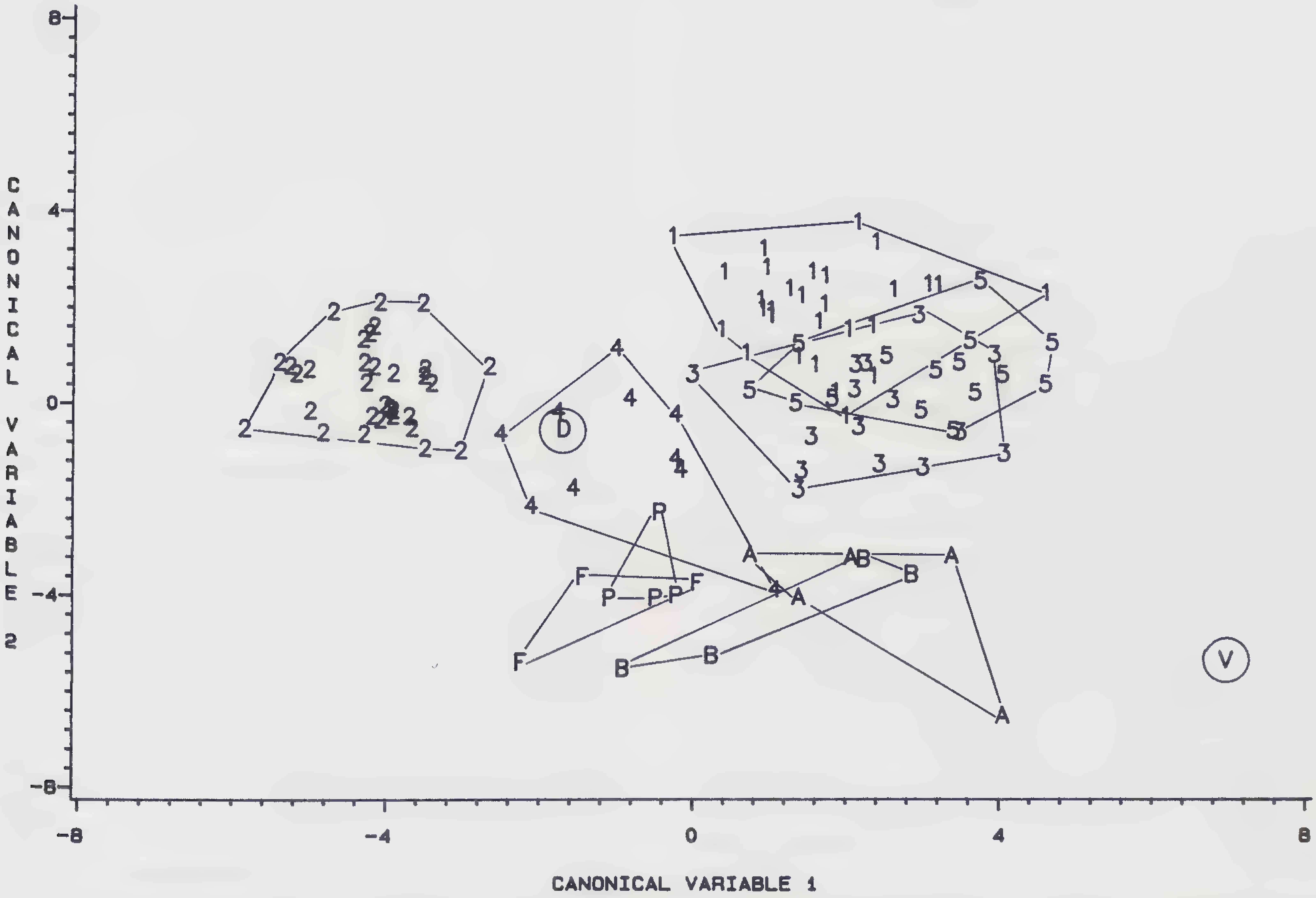
Further study of additional type material shows that the 1/3/5 species complex (*P. portoricensis, P. waylandi, P. macdonaldi,* respectively) depicted in Text-figure 10a and 17 extends into the late Oligocene, and that species 2 (*P. baracoaensis*) and 4 (*P. convivatoris*) originate during the Miocene. Apparently, the modern *P. astreoides* Lamarck, 1816, now replaces the older complex, which has a generally similar growth form and wall structure. The modern branching species (*P. porites, P. furcata* Lamarck, 1816, and *P. divaricata* Lesueur, 1821) all have a more open wall structure than their fossil counterpart, species 2 (*P. baracoaensis*).

Because of their high abundance and diversity, comparison with modern Indo-Pacific poritids is beyond the scope of the present investigation. However, it should be noted that, on preliminary examination, these fossil poritids from the Dominican Republic do not resemble any of the modern eastern Pacific poritids reported by Durham (1947).

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

The formal systematic descriptions in this section are based strictly on the results of the statistical analyses given in the previous section. Unless otherwise indicated, the synonymies include only material actually measured and statistically analyzed. A list summarizing these synonymies is given in Table 7. Following Jung (1986), the term "diagnosis" is used only



Text-figure 17.—*Porites.* Canonical discriminant analysis of the NMB fossil collections (numbered) and six modern Caribbean species (lettered). Plot of scores on the first two canonical variables showing polygons outlining the range of variation between colonies in the 11 species groups. The points represent individual colonies. 1 = *P. portoricensis,* 2 = *P. baracoaensis,* 3 = *P. waylandi,* 4 = *P. convivatoris,* 5 = *P. macdonaldi,* A = *P. astreoides* types 1–5, *P. branneri* types 14–17, D = *P. divaricata* type 13, F = *P. furcata* types 10–12, P = *P. porites* types 6–9, V = *P. verrilli* type 18. The numbers for types refer to specimens listed in Table 2.

to describe higher categories such as genera and subgenera, whereas the term "description" is reserved for complete descriptions of species, which, as discussed in the previous section, herein represent merely morphologic clusters of specimens. Lectotypes have been selected for all studied species whose primary types consist of syntypes or "cotypes".

The terminology used in the "Description" sections is defined and described in the previous section entitled "Characters". It follows the usage of Bernard (1903, 1905), Vaughan and Wells (1943), and Wells (1956). The abbreviations used in the measurements sections are explained in Tables 3 and 4. These measurements are identical to those used in the statistical analyses. Two additional characters, **CH** and **CT**, refer respectively to the colony height (in mm) and thickness (in mm).

The "Materials" sections give an approximate estimate of the amount of material in the collection of Saunders, Jung, and Biju-Duval (1986) and the number of specimens in this collection that were statistically analyzed. Species definitions are based on all of these specimens as well as on other specimens listed in the synonymies. The expression "box of fragments" is used to indicate one colony whose fragments actually fit together so that the colony could be reconstructed. Sometimes different boxes of fragments appear to belong to the same colony; however, the fragments do not fit back together. Because of this problem, estimates of possible number of colonies are also given.

The "Remarks" sections explain the synonymies only. Separate sections entitled "Variability" describe the variation within each cluster. Sections entitled "Occurrence" give detailed geographic and stratigraphic information within the studied areas of the Dominican Republic, whereas those entitled "Distribution" give general information on all known occurrences throughout the world. Unless otherwise stated, the locality numbers belong to the Naturhistorisches Museum Basel (NMB) and the material is deposited at the NMB. Assignment of formation names to individual localities is based on Saunders, Jung, and Biju-Duval (1986) (especially text-figs. 4, 6, 15, and 16), except along Río Mao where formation names are used as listed by Maury, 1919. Catalogue numbers have been assigned only to figured specimens. A unique number was given to each colony. Ages used in the "Distribution" sections are based on the following publications: Anguilla, Bold (1970); Antigua, Bold (1966); Cuba, Bold (1975); Jamaica, Zans *et al.* (1963); Puerto Rico, Frost *et al.* (1983); Chiapas, Mexico, Frost and Langenheim (1974); Florida and Georgia, Puri and Vernon (1964); Panama, Woodring (1957, 1964); Trinidad, J. B. Saunders (oral commun., 1985).

Table 7.—List of all valid poritid species described from the Miocene through Lower Pliocene of the Caribbean region, showing their current taxonomic status.

Alveopora fenestrata (Dana) of Duncan, 1863 = *P. portoricensis*
A. tampae Weisbord, 1973
Goniopora aucillana Weisbord, 1973 = *G. hilli*
G. ballistensis Weisbord, 1973 = *P. portoricensis*
G. calhounensis Weisbord, 1971
G. canalis Vaughan, 1919 = *G. hilli*
G. cascadensis Vaughan, 1919 = *P. portoricensis*
G. clevei Vaughan, 1919 = *P. portoricensis*
G. decaturensis Vaughan, 1919 = ?*G. imperatoris*
G. hilli Vaughan, 1919
G. imperatoris Vaughan, 1919
G. jacobiana Vaughan, 1919 = *G. hilli*
G. matsoni Weisbord, 1973 = *P. portoricensis*
G. panamensis Vaughan, 1919
G. tampaensis Weisbord, 1973 = *G. hilli*
Porites anguillensis Vaughan, 1919
P. astreoides Lamarck of Coryell and Ohlsen, 1929 = *P. waylandi*
P. baracoaensis Vaughan, 1919
P. carrizensis Vaughan, 1917
P. chipolanum Weisbord, 1971
P. collegniana Michelin of Duncan, 1863 = *P. waylandi*
P. convivatoris, n. sp.
P. douvillei Vaughan, 1919 = ?*P. baracoaensis*
"*P. floridaprima* Bernard" Weisbord, 1973 = *P. waylandi*
P. howei Vaughan, 1919 = ?*P. portoricensis*
P. macdonaldi Vaughan, 1919
P. portoricensis (Vaughan, 1919)
P. toulai Vaughan, 1919 = *P. baracoaensis*
P. trinitatis Vaughan, 1926
P. waylandi, nom. nov.

Family **PORITIDAE** Gray, 1842

The Poritidae are defined as colonial and hermatypic. Colonies are usually formed by extratentacular budding. Corallites (except in the *Porites* subgenera *Synaraea* Verrill, 1864, and *Napopora* Quelch, 1884) are separated by little or no coenosteum. Thecae are indistinct and flush with the tissue surface. Septa (except in *Alveopora*) consist of three to eight loosely-joined, simple, vertical trabeculae forming a meshwork of regularly-arranged pores. Septa are united horizontally by one or more rings of simple synapticulae. The innermost trabeculae of certain septa are sometimes well-developed forming paliform lobes (*sensu* Vaughan and Wells, 1943), which have been termed "pali" by most poritid workers. A single columellar trabecula is usually present. In thin-section, the calices appear shallow and obscure, and the internal skeleton consists primarily of a lattice-work or reticulum composed of vertical rods (trabeculae) and horizontal bars (septal connections and synapticulae).

Genus **PORITES** Link, 1807

Porites Link, 1807, p. 162.
Neoporites Duchassaing and Michelotti, 1866, p. 191.
Cosmoporites Duchassaing and Michelotti, 1866, p. 193.
not *Porites* Cuvier, 1798, pp. 678–679, according to Article 23b of the International Code of Zoological Nomenclature (see Veron and Pichon, 1982, p. 141).

Type species.—*Porites polymorphus* Link, 1807, p. 163 (= *Madrepora porites* Pallas, 1766 [in part], pp. 324–325). Recent, Curaçao. As discussed by Vaughan (1901) and Bernard (1905), Pallas (1766) synonymized many different branching corals including some non-*Porites* in his original description of *Madrepora porites*. The coral that Vaughan (1901) cited as actually representing *Porites porites* is the pre-Linnean *Corallium, poris stellatis* of Seba (1756, t. III, p. 202, pl. CIX, fig. 11). The location of Seba's original specimen is not known. A specimen described as topotypic is figured in Vaughan (1901, pl. 28) and in Vaughan and Wells (1943, pl. 23, fig. 2).

Diagnosis.—Colonies massive, ramose, columnar, or encrusting. Corallites usually less than 2 mm in diameter. Septa usually 12 in number, arranged in two cycles following a definite bilaterally-symmetric formula consisting of a dorsal septum, a ventral septal triplet, and four lateral septal pairs (as described by Bernard, 1905). Septa composed of one to four trabeculae, the innermost of which may form pali when thickened. Trabeculae always present in the corallite wall. A single trabecula often forms the columella.

Remarks.—The genus *Porites* occurs worldwide today in shallow, clear tropical waters and consists of more than 100 described species. It has been one of the most important reef-building corals since the beginning of the Miocene. It is abundant in all reef zones ranging from shallow nearshore areas across the reef crest to the deep forereef (Goreau, 1959), and it dominates certain nearshore areas and intermediate forereef zones (Geister, 1983). As many as five modern species are commonly recognized throughout the Caribbean region (Goreau and Wells, 1967; Wells and Lang, 1973), with the possibility of one additional species in Brazil (Verrill, 1901b). The genus is believed to have evolved during the Eocene as a result of the reduction of the third septal cycle in *Goniopora* (Bernard, 1903). Approximately 20 names have been proposed for Caribbean representatives during the Neogene.

Porites baracoaensis Vaughan

Plate 16, figures 1–13; Plate 17, figures 1–7; Plate 18, figures 1–4; Text-figures 2–5, 10, 12, 14, 16, 17

Porites baracoäensis Vaughan, 1919, pp. 499–500, pl. 147, figs. 1, 1a.
Porites baracoäensis var. *matanzasensis* Vaughan, 1919, pp. 500–501, pl. 147, figs. 2–4.
?*Porites douvillei* Vaughan, 1919, p. 501, pl. 149, figs. 2, 2a, pl. 151, figs. 1, 1a.
Porites toulai Vaughan, 1919, pp. 501–502, pl. 150, figs. 1–4.

Description.—Colony branching (branch thickness = 2.9 to 16.2 mm) to form open bushes or thickets. Calices polygonal in shape; small to intermediate in size (0.9 to 1.7 mm in diameter); shallow in depth (0.3 to 0.6 mm); with narrow, regular spacing. Theca may be elevated; composed of one (rarely two) trabeculae; straight; with weak denticles (25.9 denticles per calice). Septa 12 to 13 in number; composed of two trabeculae that form small irregular surface denticles. Septa vertically continuous. Dorsal septum relatively reduced in length. Ventral septal triplet fused. Pali usually five in number, prominent. Columella tubercle small (0.06 mm in diameter), may not be developed. Palar synapticular ring moderately-developed. Fossa narrow (0.3 to 0.5 mm).

In thin-section, vertical trabeculae and horizontal septal junctions are equally thick and well-developed. Dissepiments and synapticulae are rare. A single, prominent trabecula forms the wall without developing any coenosteal reticulum. Three thick, continuous trabeculae run down the mid-corallite region: these consist of two outermost palar trabeculae and a central columellar trabecula. Two poorly-developed trabeculae intervene between the wall and pali and form the septa.

Holotype.—USNM 325069 (refigured here: Pl. 16, fig. 4; Pl. 17, fig. 1).

Measurements of the holotype.—Means of five corallites: **CD** 1.32, **CS** 1.68, **L1** 0.428, **L2** 0.452, **L3** 0.460, **NN** 6.4, **NS** 12.0, **NB** 0.0, **DS** 1.0, **DW** 14.4, **PL** 5.2, **SR** 2.0, **WR** 1.0, **T1** 0.092, **T2** 0.120, **T3** 0.116, **SD** 0.180, **P1** 0.016, **P2** 0.304, **P3** 0.196, **C1** 0.000, **C2** 0.000, **CW** 0.586, **SY** 0.178, **WT** 0.232, **CE** 0.00, **PE** 0.38, **SE** 0.25, **WE** 0.65, **CH** 25.7, **CT** 7.4.

Type locality.—USGS locality 3476, Marl, Baracoa, Cuba. Upper Pliocene.

Lectotype of douvillei *(herein selected).*—USNM 325106 (refigured here: Pl. 16, fig. 6). Vaughan (1919, p. 501) selected two cotypes for this species, one of which cannot be found (Vaughan, 1919, pl. 151, figs. 1, 1a). The remaining specimen (Vaughan, 1919, pl. 149, figs. 2, 2a) is therefore selected as the lectotype.

Type locality of douvillei.—USGS locality 6016, La Boca Formation, Panama. Middle Miocene.

Material.—105 boxes of fragments from 41 localities representing approximately 60 colonies. 32 specimens measured.

Remarks.—Vaughan described three branched Neogene species, which he assigned to *Porites*, all with

corallite diameters of about 2 mm: (1) *P. baracoaensis,* which is distinguished by its mural shelf, thick septal granules, six thick pali, and the lack of a columella tubercle; (2) *P. douvillei,* which is distinguished by its forking septa and a columella tubercle; (3) *P. toulai,* which may lack a wall-ridge, forms series of calices, and has irregular pali and a columella tubercle. Study of the Dominican Republic material shows that these characters are all highly variable and that continuous gradational series can be recognized between all of these species as they were originally defined by Vaughan. Therefore, they are synonymized here. The species *douvillei* is only questionably synonymized, because its septal bifurcations, septal denticles, and irregular branching morphology superficially resemble those of a thin-walled *P. portoricensis.* The wall, septal granules, and pali appear thicker in the holotype of *baracoaensis* than they do in the Dominican Republic material. However, this may be the result of differential preservation.

In an undated, unpublished manuscript, Vaughan (date unknown) described one additional species from the Dominican Republic (*P. mauryi*), which also belongs to *P. baracoaensis* as defined herein. Specimens at the USNM labelled as *P. mauryi* in Vaughan's handwriting (USNM 63226) appear identical to the NMB Dominican Republic cluster.

Re-examination of the Tertiary Puerto Rican corals described by Coryell and Ohlsen (1929) shows that only one specimen belongs to *P. baracoaensis*: AMNH 23085 (*P. toulai*) from the Lares Formation.

Porites chipolanum Weisbord, 1971 (pp. 20–22, pl. 4, figs. 7, 8, pl. 5, figs. 1, 2) (FSU CH5-5a) resembles *P. baracoaensis* in branching morphology and cerioid wall structure. However, the larger, deeper calices, five prominent pali, and small columella tubercle of *P. chipolanum* are more strongly suggestive of the modern Caribbean species *P. porites* (Pallas, 1766).

No specimens of *P. baracoaensis* as defined herein appear to be represented in the Frost and Langenheim (1974) material from Chiapas, Mexico. Specimens of *P. douvillei* (UI X3565–X3571) from the Oligocene La Quinta Formation of Chiapas are distinctly different from Vaughan's (1919) *P. douvillei* and from the NMB *P. baracoaensis* in that they have larger, shallower corallites, more septa, more pali, more (although thinner) synapticulae, larger columellae, and thicker walls.

Variability.—Porites baracoaensis is probably the least variable of all species studied. Although sometimes less than 5 mm, branch thickness averages a constant 8 to 10 mm throughout the section studied (Text-fig. 5a). Although corallite diameter decreases most frequently upsection, it shifts in direction sporadically yielding no definite trend (Text-fig. 4b). On the other hand, wall structure remains fairly constant upsection (Text-fig. 4a). Within a colony, corallites appear larger and more heavily calcified near the colony base.

Comparison.—Porites baracoaensis is distinctly different from all the other Neogene Dominican Republic *Porites* because of its small, shallow corallites, its thin, more solid walls, its prominent pali, and its uniform branching morphology. It somewhat resembles the modern Caribbean species *P. furcata* Lamarck, 1816, in its branching morphology and wall structure. The major difference between the two species lies in the shallower calices with more prominent columella tubercles in *P. baracoaensis.* Statistical tests, therefore, show that the two species are clearly distinct (Text-fig. 17). As shown on Text-figure 16a, only one Miocene Mediterranean species (*P. mancietensis* Chevalier, 1961) is similar to *P. baracoaensis.* Like *P. baracoaensis, P. mancietensis* has fairly small corallites, thin solid walls lacking coenosteal reticulum, shallow calices, and well-developed pali. *Porites mancietensis,* however, forms small encrusting knobs, whereas *P. baracoaensis* is branching with uniform long, thin branches.

Occurrence.—Río Cana: Cercado Formation (NMB locs. 16853, 16856, 17004), Gurabo Formation (NMB locs. 16826, 16861, 16863, 16881), and Mao Formation (NMB locs. 16884, 16885). Río Gurabo: Gurabo Formation (NMB locs. 15806, 15808, 15814, 15837, 15838, 15839, 15840, 15842, 15844, 15845, 15846, 15849, 15850, 15851, 15853, 15856, 15858, 15859, 15862, 15863, 16811, 16882, 16883, 16921, 16934) and Mao Formation (NMB locs. 15822, 15824, 15826, 15830, 15834, 16122). Río Mao: ?Gurabo Formation (NMB loc. 16911).

Distribution.—Porites baracoaensis has been found widely distributed across the central Caribbean during Neogene time. It occurs outside the Dominican Republic in the following strata: (1) Lower Miocene Lares Formation of Puerto Rico; (2) Middle Miocene La Boca Formation of Panama; and (3) Upper Pliocene La Cruz and Baracoa formations of Cuba, Bowden Formation of Jamaica.

Porites convivatoris, new species
Plate 19, figures 1–13; Plate 20, figures 1–4,
Text-figures 2–5, 10, 12, 14, 16, 17

Etymology of the name.—L. *convivator* = host; genitive singular.

Description.—Colony ellipsoidal; small (length = 5.5 to 14.8 mm, width = 3.7 to 9.2 mm); smooth surface; a calcareous tube (approximately 2 mm in diameter) always extends down the long axis of the colony. The tube is 0.2 to 0.5 mm in thickness with faint concentric growth layering and is minutely porous in texture. The

epitheca of the coral extends to the tube edges wherever the tube protrudes beyond the outer colony surface. Calices polygonal, intermediate in size (1.0 to 1.6 mm in diameter), deep (0.6 to 1.0 mm) with narrow, regular spacing. Theca sinuous, often zigzag in outline, composed of one to two trabeculae with prominent denticles (mean = 25.3 denticles per calice). Septa 12 in number, composed of two non-palar trabeculae that form small, irregular surface denticles. The uppermost septal surface consists of horizontal flakes, often bifurcating near the wall. Dorsal septum relatively reduced in length. Ventral septal triplet fused. Pali weak, irregular, three to five in number. Dorsal palus absent. Columella tubercle present, weakly-developed. Palar synapticular ring poorly-developed. Fossa narrow (0.3 to 0.5 mm).

In thin-section, vertical thecal trabeculae are prominent; horizontal septal junctions are thin and poorly-developed; dissepiments are abundant; and synapticulae are common. A single prominent trabecula forms the wall, accompanied by occasional coenosteal reticulum. Two or three trabeculae run down the mid-corallite region: the two outermost form pali that are irregular and discontinuous and the third, when developed, forms the columella, which is solid and continuous. Two poorly-developed trabeculae intervening between the wall and mid-corallite region form the septa.

Holotype.—NMB D5830 (figured here: Pl. 19, figs. 1, 7).

Measurements of the holotype.—Means of five corallites: **CD** 1.52, **CS** 1.51, **L1** 0.396, **L2** 0.568, **L3** 0.608, **NN** 6.6, **NS** 12.0, **NB** 4.8, **DS** 1.8, **DW** 24.0, **PL** 4.6, **SR** 2.0, **WR** 1.0, **T1** 0.080, **T2** 0.080, **T3** 0.120, **SD** 0.136, **P1** 0.000, **P2** 0.140, **P3** 0.120, **C1** 0.156, **C2** 0.088, **CW** 0.460, **SY** 0.118, **WT** 0.168, **CE** 0.27, **PE** 0.42, **SE** 0.52, **WE** 0.69, **CH** 9.2, **CT** 10.0.

Type locality.—NMB locality 16852, Río Cana, Cercado Formation, Dominican Republic. Upper Miocene (Saunders, Jung, and Biju-Duval, 1986, text-fig. 15).

Paratypes.—NMB D5831–D5841 (figured here: Pl. 19, figs. 2, 3, 6, 8–13; Pl. 20, figs. 1–4).

Material.—191 colonies from 15 localities. Ten specimens measured.

Remarks.—This species was described by T. W. Vaughan in an unpublished manuscript under the name *Porites dominicensis.* The manuscript was recently found in a drawer in the Vaughan collection at the USNM and is now archived at the USGS library in Denver. I have not been able to locate the exact material on which this description was based.

Calcareous tubes similar to those characteristic of this species are formed today by a sipunculid worm, *Aspidosiphon corallicola* Sluiter, 1889, commensal with the coral *Heteropsammia cochlea* (Spengler, 1781), which inhabits muddy areas of the Great Barrier Reef (see Goreau and Yonge, 1968). As the worm moves, it carries the coral to new feeding areas, often covering a distance of up to one meter in a 24-hour period.

Variability.—Although the colony is consistently small and ellipsoidal in shape (Text-fig. 5b), corallite characters do vary widely following few clear trends. Wall structure remains fairly constant stratigraphically upsection (Text-fig. 4a), whereas corallite diameters tend to decrease very slightly (Text-fig. 4b). Similarly, within colonies, corallite diameters decrease from colony center to edge; however, such variation may be more strongly related to ontogeny than to environment. Because of the small size of the colony, other within-colony trends are not apparent.

Comparison.—*Porites convivatoris* is unique among the Neogene Caribbean *Porites* in its small colony size and its unusual ellipsoidal colony shape with a tube extending down the long axis. It also differs in its highly elevated, intermediate-sized calices, which have thin walls, a small columella, and four to five prominent pali. As shown by Text-figure 17, *P. convivatoris* has calices that resemble those of at least three modern Caribbean species: the finely-branching *P. divaricata* Lesueur, 1821, the thickly-branching *P. porites* (Pallas, 1766), and the encrusting to massive *P. branneri* Rathbun, 1887. However, *P. convivatoris* clearly differs from these three modern forms in its better-developed columellar tubercle, weaker pali, and its thicker, bifurcated septa.

As shown in Text-figure 16a, four described Miocene Mediterranean species all closely resemble *P. convivatoris*: *P. collegniana* Michelin, 1842, *P. incrustans* Milne-Edwards and Haime, 1851, *P. leptoclada* Reuss, 1872, and *P. lobatosepta* Chevalier, 1961. All have closely-spaced, intermediate-sized calices with high elevations and well-developed pali and columellae. The septa have numerous denticles and frequently bifurcate. None of these Mediterranean species, however, form small ellipsoidal colonies with a tube extending down the long axis. *Porites collegniana* and *P. incrustans* form intermediate to large encrusting colonies, and *P. lobatosepta* and *P. leptoclada* are typically branching.

Occurrence.—Río Cana: Cercado Formation (NMB locs. 16836, 16839, 16844, 16852, 16984, 16986) and Gurabo Formation (NMB loc. 16879). Río Mao: Cercado Formation (NMB locs. 16913, 16915, 16916, 16918, 16922, 16926, 16928, 16929).

Distribution.—This species is not known from outside the Upper Miocene and Lower Pliocene of the Dominican Republic.

Porites macdonaldi Vaughan

Plate 21, figures 1–8; Plate 22, figures 1–6; Plate 23, figures 1–4; Text-figures 2–5, 10, 12, 14, 16, 17, 19

?*Porites anguillensis* Vaughan, 1919, pp. 504–505, pl. 150, fig. 5; not pl. 149, figs. 1, 1a, 1b.

Porites (*Synaraea*) *macdonaldi* Vaughan, 1919, pp. 506–507, pl. 152, figs. 1–4.

Description.—Colonies columnar, massive, or plate-shaped. Plates 3.5 to 15 mm thick, with faint growth bands at 2- to 3-mm intervals. Epitheca having numerous linear striations (0.2 to 0.3 mm thick, spaced 1.5 mm apart, and oriented parallel to the direction of growth). Calices circular in shape; intermediate in size (1.1 to 1.6 mm in diameter) and in depth (0.4 to 0.9 mm); with wide, irregular spacing. Frequently intratentacular budding forms corallite rows separated by ridges of coenosteum. Theca composed of three to six trabeculae forming a characteristic costal reticulum; sinuous; with weakly-developed denticles (22.1 denticles per calice). Septa 12 to 13 in number; composed of three non-palar trabeculae that form small, irregular surface denticles. Septa vertically continuous; of equal length and thickness. Ventral septal triplet fused. Pali weak, zero to five in number. Columella tubercle usually present, moderately-developed. Palar synapticular ring poorly-developed. Fossa of moderate width (0.4 to 0.6 mm).

In longitudinal thin-section, horizontal septal junctions are thick and predominant, whereas vertical trabeculae are weak. The dissepiments and synapticulae are well-developed. The corallite wall consists of one to two vertical trabeculae that intergrade with an extensive, irregular coenosteal reticulum. The columella is formed by a tangle of one to two discontinuous vertical trabeculae that can be traced down the corallum. The septa are composed of two weak trabeculae. In tangential sections, an irregular arrangement of thick, relatively solid corallite walls incompletely surrounds groups of elliptical speck-like denticles or lobes. The inner circle of these specks is consistently six in number and surrounds a single similarly-shaped columella tubercle.

Lectotype (herein selected).—USNM 72376, one of the original cotypes designated and figured by Vaughan (1919, pl. 152, fig. 1). Paralectotypes consist of three additional cotypes (USNM 325046) designated and figured by Vaughan (1919, pl. 152, figs. 2, 3, 3a, 4). The calices of all four type specimens appear to be distorted considerably by subsequent geologic compression of the reefal unit at the type locality in the Emperador Limestone. A fifth possible specimen of this species, which was not designated as a cotype but was figured by Vaughan (1919, pl. 152, figs. 5, 5a), has not been found. The lectotype and one paralectotype are refigured on Plate 21, figures 1, 4 and on Plate 22, figure 1.

Measurements of the lectotype.—Means of five corallites: **CD** 1.33, **CS** 1.89, **L1** 0.440, **L2** 0.460, **L3** 0.512, **NN** 7.4, **NS** 12.4, **NB** 2.0, **DS** 2.0, **DW** 23.2 **PL** 5.0, **SR** 3.4, **WR** 2.8, **T1** 0.108, **T2** 0.116, **T3** 0.124, **SD** 0.120, **P1** 0.000, **P2** 0.120, **P3** 0.116, **C1** 0.172, **C2** 0.132, **CW** 0.522, **SY** 0.102, **WT** 0.444, **CE** 0.229, **PE** 0.287, **SE** 0.325, **WE** 0.688, **CH** 11.2, **CT** 55.9.

Type locality.—USGS locality 6016, Empire Quarry, Emperador Limestone of the La Boca Formation of Panama. Middle Miocene.

Material.—80 boxes of fragments from 20 localities, representing approximately 80 colonies. 14 specimens measured.

Remarks.—This species was originally assigned to the subgenus *Synaraea* Verrill, 1864 by Vaughan (1919), because of its well-developed coenosteal reticulum. However, its calices are distinctly larger (1 to 1.5 mm in diameter) than other modern representatives of *Synaraea,* which usually have calices less than 1 mm in diameter. Additionally, the pronounced coenosteal ridges between corallites on the fossil specimens are more characteristic of the subgenus *Napopora* Quelch, 1884, than they are of *Synaraea,* which tends

Text-figure 18.—Surface of a modern colony of *Porites astreoides* having a *Synaraea*-like appearance, ×16. The corallites of this coral sometimes appear reduced in size and separated by a well-developed wall reticulum in forereef habitats at moderate depths. Wells personal collection #1332, Discovery Bay, 20 m, Jamaica. (Photo courtesy of J. W. Wells)

to develop more superficial corallites that are flush on the surface of the corallum. The subgenus *Napopora* is poorly known and has never been reported as a fossil or in the Caribbean (Veron and Pichon, 1982). Due to these ambiguities, *P. macdonaldi* has not been assigned to a separate subgenus and is herein considered *Porites sensu stricto*. Results of the canonical variable analyses (Text-fig. 10a) show that *P. macdonaldi* does not differ enough from *P. portoricensis* (Vaughan, 1919) or *P. waylandi*, nom. nov., to warrant separation into a distinct subgenus. Also, some modern Caribbean specimens of *Porites astreoides* Lamarck, 1816, have been found to develop similar small-sized calices separated by extensive coenosteal reticulum in deep, low-light environments (Text-fig. 18).

A paratype of *P. anguillensis* (USNM 325103) is questionably included in the synonymy, because its surface is so badly preserved that corallites can hardly be distinguished. Like the holotype of *P. anguillensis* (PIU WI-43), it is plate-shaped; however, it does not have the large calices with six prominent pali and the well-developed columella tubercle that are characteristic of the holotype. The paratype appears to have more superficial corallites with a well-developed coenosteal reticulum and therefore more likely belongs to *P. macdonaldi.*

The Oligocene Chiapas (Mexico) specimen of Frost and Langenheim (1974) referred to as *Porites* (*Synaraea*) *macdonaldi* (UCMP 10239, pls. 7–8, figs. 4–5), is lost. From the description and photographs given by Frost and Langenheim (1974), their specimen appears to belong to *P. macdonaldi* as described here.

Variability.—Although the colony shape is uniformly plate-like (Text-fig. 5b), all corallite characters (especially pali number) (Text-fig. 14c) do vary moderately, however following no significant trends. Wall thickness appears to decrease slightly upsection stratigraphically (Text-fig. 4a) accompanied by slight increase in corallite diameter (Text-fig. 4b). Within colonies, the coenosteal reticulum is better-developed along the colony edge.

Comparison.—*Porites macdonaldi* is not similar to any other modern Caribbean or Miocene Mediterranean species. As explained in the "Comparison" section for *P. portoricensis,* it most closely resembles the Neogene Caribbean species *P. portoricensis* and *P. waylandi.* It differs from these two species in its relatively small corallite diameter, wide columellar synapticular ring, well-developed pali, less pronounced ornamentation, and fewer septa.

Occurrence.— Río Cana: Gurabo Formation (NMB locs. 16815, 16823, 16826, 16861, 16881). Río Gurabo: Gurabo Formation (NMB locs. 15837, 15841, 15846, 15851, 15852, 15855, 15857, 16811, 16882, 16883, 16921, 16933) and Mao Formation (NMB locs. 15824, 15826). Río Mao: ?Gurabo Formation (NMB loc. 16911).

Distribution.—*Porites macdonaldi* ranges in age from late Oligocene to early Pliocene and has been found widely distributed across the central Caribbean. Outside of the Dominican Republic, it occurs in the following strata: (1) Upper Oligocene La Quinta Formation of Chiapas, Mexico; (2) Lower Miocene Anguilla Formation of Anguilla; and (3) Middle Miocene La Boca Formation of Panama.

Porites portoricensis (Vaughan)
Plate 24, figures 1–15; Plate 25, figures 1–6;
Plate 26, figures 1–6; Plate 27, figures 1–4; Plate 28, figures 1–4; Text-figures 2–5, 10, 12, 14, 16–19

not *Alveopora fenestrata* (Lamarck) Dana, 1846, p. 98.
Alveopora fenestrata (Dana) Duncan, 1863, p. 437.
Goniopora portoricensis Vaughan, 1919, pp. 495–496, pl. 146, figs. 4, 5.
Goniopora clevei Vaughan, 1919, pp. 496–497, pl. 145, figs. 1, 3–6a; ?pl. 145, figs. 2, 2a.
Goniopora cascadensis Vaughan, 1919, pp. 497–498, pl. 146, figs. 6–9.
?*Porites* (*Synaraea*) *howei* Vaughan, 1919, pp. 505–506, pl. 151, figs. 2–4.
Goniopora ballistensis Weisbord, 1973, p. 32, pl. 11, figs. 1–3; pl. 10, figs. 4, 5 (seen); ?pl. 12, figs. 1, 2 (not seen).
Goniopora matsoni Weisbord, 1973, p. 34, pl. 12, fig. 3; pl. 12, figs. 4–6 (seen); pl. 14, figs. 1–3 (not seen).

Description.—Colony irregularly branching or columnar (6 to 52 mm thick) with skirted margins that may form plates. Colony surface generally smooth with occasional lumps or protuberances. Calices polygonal to circular, highly variable in size (1.2 to 2.2 mm in diameter) with intermediate depths (0.3 to 1.0 mm) and variable, and in some specimens irregular spacing. Occasional intratentacular budding forming short corallite rows and rare ridges in the coenosteum may give the coral a *Napopora*-like appearance. Theca composed of two to five trabeculae commonly form a costal reticulum; sinuous, sometimes zigzag in outline; with prominent granulations (mean = 24.2 granulations per calice). Septa 11 to 13 in number; composed of two to three non-palar trabeculae, the innermost of which commonly develops a large denticle. Septa relatively thick (>0.1 mm). Septal surface consisting of horizontal flakes, commonly bifurcating near the wall. Septa of equal length and thickness. Ventral septal triplet free or fused. Pali poorly-developed, if at all. Columella tubercle well-developed. Palar synapticular ring well-developed. Fossa of moderate width (0.4 to 0.7 mm).

In longitudinal thin-section, horizontal septal junctions predominate. They are uniformly widely-spaced and well-developed and are interrupted only occasion-

ally by thinner, irregular vertical trabeculae. Dissepiments and synapticulae are rare. Commonly three trabeculae form the corallite wall; however, this structure cannot be traced far below the surface into the corallum. The columella is formed by an irregular tangle of two to three trabeculae. In tangential section, the septal denticles form a characteristic circle of six to eight oval specks, and the septa are composed of two to three thick, irregular trabeculae. The reticulum at the core of the branch axis is especially porous and dominated by vertical structures.

Holotype.—USNM 325061 (refigured here: Pl. 24, fig. 1; Pl. 25, fig. 1).

Measurements of the holotype.—Means of five corallites: **CD** 1.42, **CS** 1.88, **L1** 0.344, **L2** 0.400, **L3** 0.432, **NN** 7.0, **NS** 12.2, **NB** 2.4, **DS** 3.2, **DW** 26.6, **PL** 5.6, **SR** 3.4, **WR** 2.8, **T1** 0.076, **T2** 0.072, **T3** 0.060, **SD** 0.092, **P1** 0.068, **P2** 0.128, **P3** 0.104, **C1** 0.212, **C2** 0.100, **CW** 0.544, **SY** 0.080, **WT** 0.416, **CE** 0.19, **PE** 0.25, **SE** 0.27, **WE** 0.42, **CH** 74.3, **CT** 6.0.

Type locality.—USGS locality 3191, Lares Formation, four miles west of Lares, Puerto Rico. Lower Miocene.

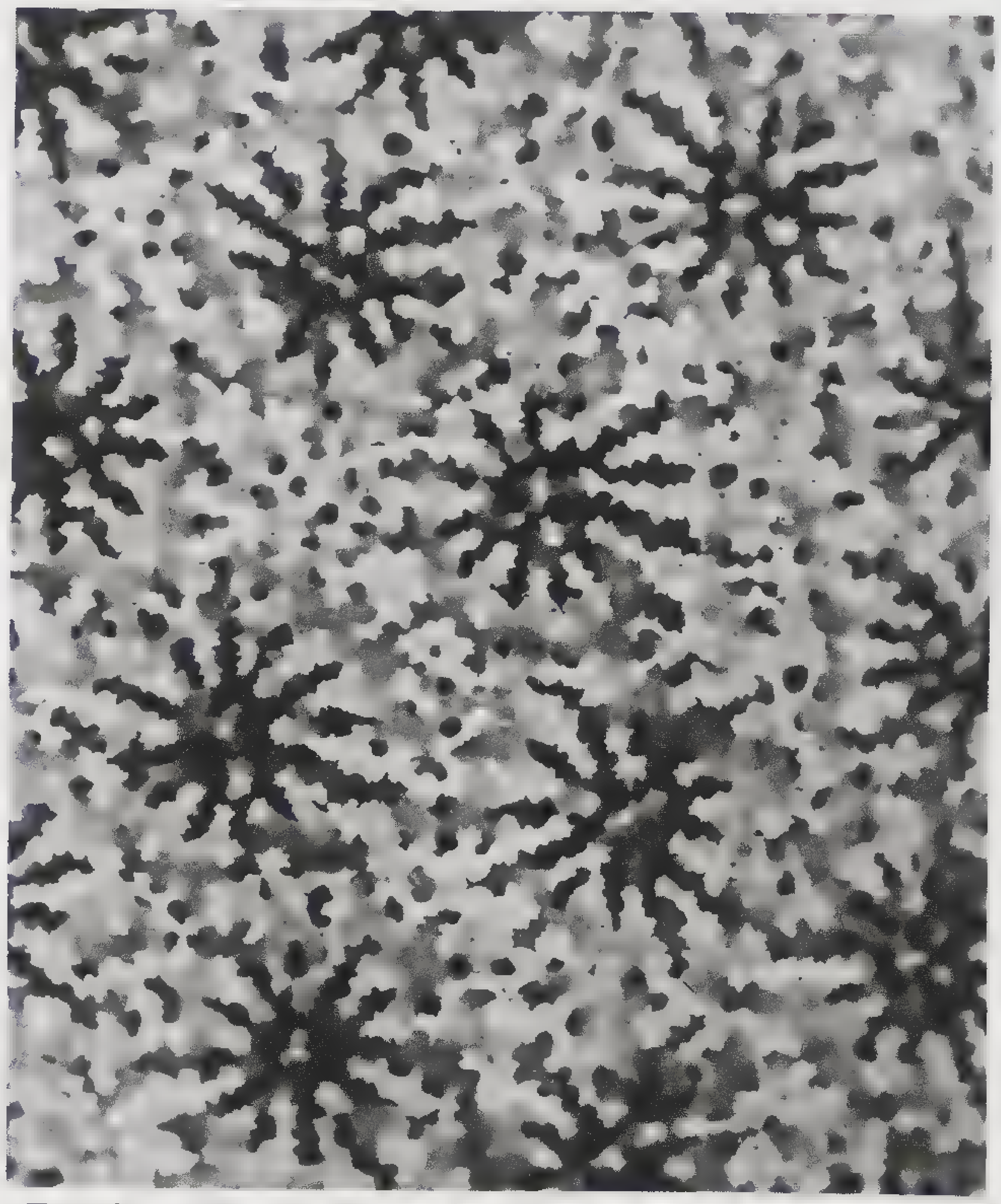
Lectotype of howei *(herein selected).*— USNM 72890 (refigured here: Pl. 24, fig. 6). Vaughan (1919, pp. 506–507) designated three cotypes for this species, one of which has been selected as the lectotype (Vaughan, 1919, pl. 151, fig. 4). The remaining two of his original cotypes, USNM 325113 (Vaughan, 1919, pl. 151, figs. 2, 3), are selected as paralectotypes.

Type locality of howei.—USGS locality 6016, La Boca Formation, Panama. Middle Miocene.

Material.—133 boxes of fragments from 35 localities, representing approximately 60 colonies. 30 specimens measured.

Remarks.—Study of the Dominican Republic material shows that this species is highly variable. Consequently, three and possibly four of Vaughan's (1919) original Neogene Caribbean species of the Poritidae are synonymized. Vaughan originally described three of these species as belonging to the genus *Goniopora* Blainville, 1830, because bifurcations of the first two septal cycles suggested the presence of a third poorly-developed septal cycle. However in the Dominican Republic material, these bifurcations appear to be related to decreased calcification in the centers of horizontal septal flakes near the wall and not to the actual development of tertiary septa. Similar horizontal flakes have been found to develop in modern Caribbean specimens of *P. astreoides* Lamarck, 1816 in low-light environments (Text-fig. 19). The overall septal arrangement also clearly follows a *Porites* pattern, consisting of four lateral septal pairs and a ventral septal triplet. The *Goniopora* pattern of fusion of the tertiary septa with the secondary septa cannot be recognized. Bifurcations can be seen in both primary and secondary septa (see Pl. 28, figs. 1, 2).

The four Vaughan species (*portoricensis, clevei, cascadensis,* and *howei*) were all originally described as branching forms with large corallite diameters (approx. 2 mm), variably-developed mural reticula, thick granules or denticles on the upper surface of septal trabeculae, and a dense columella. The species *portoricensis* was originally characterized by thinner, more delicate septal denticles and columellae. In *clevei,* the upper surface of the innermost septal trabeculae were described as thickened to form pali. In *cascadensis,* three prominent rows of septal granules were developed and the mural reticulum was reduced in thickness, in some specimens forming a zigzag wall ridge. Study of the Dominican Republic material shows that all of these characters vary continuously in *P. portoricensis,* even across the surface of a single colony, and that they therefore do not warrant species-diagnostic status. Furthermore, although it is not complete, the canonical variable polygons of the types of *portoricensis, clevei,* and *cascadensis* clearly overlap with the Dominican Republic *portoricensis* polygon (Text-fig. 10). Unfortunately, the holotype of *P. portoricensis* has been compressed due to geologic compaction and lies statisti-



Text-figure 19.—Surface of a modern colony of *Porites astreoides* with flaky septa, ×16. The septa in this coral appear to be formed by horizontal flakes in deep-water habitats. Wells personal collection #2241, Discovery Bay forereef, 42 m, Jamaica. (Photo courtesy of J. W. Wells)

cally at the margin of the Dominican Republic *portoricensis* cluster. Therefore, it makes a poor representative of the species.

Vaughan's species *howei* is questionably synonymized with the Dominican Republic *portoricensis* material. The type material for *howei* is poorly preserved and distorted by geologic compaction. The cluster of its types is discrete, but it is nevertheless close enough to the Dominican Republic group still to represent the same species. It differs from the Dominican Republic cluster by having smaller calices (mean corallite diameter = 1.134 mm) and a more extensive reticulum. Six pali are commonly developed by the innermost septal trabeculae. The species *howei* forms subpalmate branches with carinae that may be characteristic of the Dominican Republic specimens (*e.g.*, NMB D5796, Pl. 24, fig. 7; Pl. 26, fig. 3).

The statistical analyses show that a paratype of Weisbord's (1973) species *ballistensis* (USNM 68314) clearly falls within the cluster of *clevei* types, and the holotype of *matsoni* (USNM 68315) falls within the cluster of Dominican Republic *portoricensis* (Text-fig. 10); therefore, both Weisbord species are included in the synonymy. Similarly, Duncan's (1863) specimen of *Alveopora fenestrata* [BM(NH) R28828] falls within the Dominican Republic *portoricensis* cluster and is also synonymized.

Re-examination of the Tertiary Puerto Rican corals described by Coryell and Ohlsen (1929) shows that specimens of five described species belong to *P. portoricensis*: AMNH 23085 (*P. toulai* Vaughan, 1919), AMNH 23054 (*G. portoricensis*), AMNH 23042 (*G. clevei*), and AMNH 23078 (*P. douvillei* Vaughan, 1919) from the Lares Formation, and AMNH 23076 (*P. baracoaensis* Vaughan, 1919) from the Ponce Formation.

Frost and Langenheim's (1974) figured material of *P. baracoaensis* (pl. 77, figs. 1–5, UI X3592–X3596) and of *Goniopora cascadensis* (pl. 79, figs. 3–7, UI X3598–X3599) has been lost. However, the photos and descriptions of these two species closely conform to the concept of *P. portoricensis* described herein.

Variability.—*Porites portoricensis* is the most variable of all the species studied; however, consistent trends of variation are extremely complex and therefore difficult to recognize. Colony morphology, corallite size, wall structure, and the development of the coenosteal reticulum all vary widely. Within colonies, corallites are smaller and the coenosteal reticulum better-developed in thicker columns near the colony base. Only insignificant trends can be detected up the stratigraphic section. Branch thickness increases somewhat upsection (Text-fig. 5) accompanied by a corresponding decrease in corallite diameter and slight decrease in wall thickness (Text-fig. 4).

Comparison.—This species appears to be unique among branched Neogene Caribbean *Porites* by having large corallites, bifurcated septa, a thick mural reticulum, and thickened septal denticles and/or pali. It appears to be most closely related to the two massive species of *Porites* represented in the Dominican Republic material; however, it differs from both *P. waylandi* and *P. macdonaldi* by having larger corallites, thicker septa, and numerous prominent septal denticles. *Porites portoricensis* does not resemble any Miocene Mediterranean species or any modern Caribbean species.

Occurrence.— Río Cana: Cercado Formation (NMB locs. 16853, 16856), Gurabo Formation (NMB locs. 16815, 16823, 16826, 16881), and Mao Formation (NMB locs. 16884, 16885). Río Gurabo: Gurabo Formation (NMB locs. 15808, 15837, 15838, 15840, 15845, 15849, 15850, 15851, 15853, 15855, 15893, 16184, 16811, 16882, 16883, 16921, 16933, 16934) and Mao Formation (NMB locs. 15821, 15822, 15824, 15826, 15834). Río Mao: ?Gurabo Formation (NMB loc. 16911). Río Yaque del Norte: Tabera Group (NMB locs. 16909, 17279), Baitoa Formation (NMB loc. 17277).

Distribution.—*P. portoricensis* ranges in age from late Oligocene to early Pliocene and has been found widely distributed throughout the Caribbean. The occurrences in the Dominican Republic are the youngest reported for the species. It has been found outside the Dominican Republic in the following strata: (1) Upper Oligocene Antigua Formation of Antigua and La Quinta Formation of Chiapas, Mexico; (2) Lower Miocene Anguilla Formation of Anguilla, Santa Ana Formation of Chiapas, Mexico, and Tampa Formation of Florida; and (3) Middle Miocene La Boca Formation of Panama and Ponce Formation of Puerto Rico.

Porites waylandi, nom. nov.

Plate 29, figures 1–4; Plate 30, figures 1–7; Plate 31, figures 1–4; Text-figures 2–5, 10, 12, 14, 16, 17

not *Porites collegniana* Michelin, 1842, p. 65, pl. 13, fig. 9.
Porites collegniana Michelin. Duncan, 1863, p. 437.
not *Porites panamensis* Verrill, 1866, p. 329.
Porites panamensis Vaughan, 1919, pp. 503–504, pl. 148, figs. 1–3a (junior homonym).
"*Porites floridaprima* Bernard" of Weisbord, 1973, pp. 28–29 (in part), unfigured mentioned specimen and ?pl. 8, figs. 1–3 (seen); ?pl. 9, figs. 1–4 and ?pl. 10, figs. 1–3 (not seen).

Description.—Colony columnar, massive, or plate-shaped, with distinct growth bands at 4- to 6-mm intervals. Colony surface generally smooth with occasional lumps or protuberances. Calices polygonal, intermediate in size (1.2 to 1.8 mm in diameter) with intermediate depths (0.4 to 1.0 mm), having intermediate, regular spacing. Some theca elevated; com-

posed of two to five trabeculae; sinuous, usually zigzag; with moderate-sized denticles (19.6 denticles per calice). Septa 12 in number; composed of two trabeculae that form small to moderate-sized surface denticles. Septa vertically continuous with bifurcations near the wall. Septa of equal length and thickness. Ventral septal triplet fused. Pali poorly-developed, usually four in number. Columella tubercle well-developed (0.1 to 0.3 mm thick). Palar synapticular ring moderately-developed. Fossa relatively wide (0.5 to 0.8 mm).

In longitudinal thin-section, vertical trabeculae and horizontal septal junctions are uniformly widely-spaced and equally thin, forming an open network. Synapticulae, dissepiments, and trabeculae around the columella are especially well-developed. Corallites are separated by an even coenosteal reticulum. The wall is formed by a thick vertical trabecula whose extent can be traced through the corallum. The columella is composed of three to four thin vertical trabeculae and the septa of two poorly-developed trabeculae. In tangential section, the septa extend to the columellar synapticular ring. The wall is open and continuous with a regular coenosteal reticulum.

Holotype.—USNM 325063 (refigured here: Pl. 29, fig. 1; Pl. 30, fig. 1).

Measurements of the holotype.—Means of five corallites: **CD** 1.64, **CS** 1.85, **L1** 0.564, **L2** 0.784, **L3** 0.616, **NN** 7.0, **NS** 11.6, **NB** 1.6, **DS** 2.00, **DW** 17.2, **PL** 5.2, **SR** 3.0, **WR** 1.8, **T1** 0.140, **T2** 0.132, **T3** 0.128, **SD** 0.152, **P1** 0.072, **P2** 0.148, **P3** 0.160, **C1** 0.168, **C2** 0.136, **CW** 0.710, **SY** 0.148, **WT** 0.420, **CE** 0.15, **PE** 0.36, **SE** 0.36, **WE** 0.73, **CH** 23.6, **CT** 89.1.

Type locality.—USGS locality 6015, Empire Quarry, La Boca Formation, Panama. Middle Miocene.

Material.—39 boxes of fragments from 22 localities, representing approximately 30 colonies. 16 specimens measured.

Remarks.—Vaughan (1919) originally described and named this Neogene coral *Porites panamensis,* apparently unaware of Verrill's (1866) description of the living eastern Pacific species *Porites panamensis.* The fossil clearly differs from the living coral in corallite size and in the structure of the wall and columella. The fossil has distinctively larger corallites, a better-developed coenosteal reticulum, and a thick columella. Therefore, Vaughan's (1919) fossil species is herein renamed "*waylandi*" after Vaughan's middle name.

Vaughan (1919, and *in* Vaughan and Hoffmeister, 1926) described three species of massive Miocene *Porites* having corallite diameters of 1.5 to 2 mm and some (although thin) coenosteal reticula: (1) *P. panamensis* Vaughan, 1919, with small to intermediate-sized corallite diameters and an irregular wall structure, apparently produced by intratentacular budding, (2) *P. anguillensis* Vaughan, 1919, with large corallite diameters and a regular coenosteal reticulum, and (3) *P. trinitatis* Vaughan, *in* Vaughan and Hoffmeister, 1926, with small corallite diameters and a thin, solid wall forming no coenosteal reticulum. In addition, "*panamensis*" was defined as having six pali, thin synapticulae, and a thin columella tubercle; *anguillensis* as forming flexed laminar plates and having a directive triplet that fuses near the columella, numerous synapticulae and a well-developed columella tubercle, and five to six prominent pali; and *trinitatis* as having thin synapticulae, a thin columella tubercle, six pali, and a directive triplet that fuses at the ventral palus. As shown by Text-figures 10b and 12b respectively, *trinitatis* and *anguillensis* are statistically different from "*panamensis*". The three species, therefore, are not synonymized.

Although the "holotype" [BM(NH) R2343] represents an unusual branching form, most of Weisbord's (1973) specimens of "*P. floridaprima* Bernard" clearly fall into the NMB *waylandi* cluster (Text-fig. 12b). This includes the specimen measured herein (USNM 66220) as well as other USNM specimens labelled by Vaughan as "*Porites willcoxi*" from USGS locality 3286 (Ballast Point, Tampa, Florida). Vaughan described *P. willcoxi* neither in publication nor, to my knowledge, in manuscript. Weisbord's (1973) use of Bernard's (1906, p. 71, pl. 12, fig. 2) description to name the species "*floridaprima*" is cited in quotation marks here, because Bernard (1906) did not use Linnean nomenclature in describing the coral and therefore Bernard's (1906) name is invalid. Also for the same reason, the new taxa described in Bernard's (1903, 1905, 1906) three monographs on the Poritidae should be placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature.

Re-examination of the Tertiary Puerto Rican corals described by Coryell and Ohlsen (1929) shows that specimens of three described species belong to *P. waylandi*: AMNH 23081 (*P. panamensis*) from Lares, AMNH 23074 (*P. astreoides* Lamarck, 1816) from Guanica, and AMNH 23077 and AMNH 23079 (*P. douvillei* Vaughan, 1919) from Lares.

Frost and Langenheim's (1974) specimens of *P. panamensis* (UI X3537–X3562) are lost. Nevertheless, their description and photos closely resemble *waylandi* as described herein. In addition, study of some of Frost and Langenheim's (1974) specimens of *P. trinitatis* (UI X3576 and X3585) shows that their colony shape and wall structure are similar to *P. waylandi.* However, the corallites are distinctively small (the mean corallite diameter for UI X3583 is 1.16 mm), and the septa, pali, columellae, and synapticulae are particularly thin.

Variability.—*Porites waylandi* has relatively stable corallite characters, the most variable being wall thick-

ness and the development of the pali. Corallite diameter increases slightly upsection (Text-fig. 4b) and changes in colony height (Text-fig. 5b) appear positively correlated with wall thickness (Text-fig. 4a). Within colonies, corallites appear larger and more widely-spaced from colony top to side.

Comparison.—As discussed in the "Comparison" section for *P. portoricensis* (Vaughan, 1919), of all Neogene Caribbean species of *Porites, P. waylandi* most closely resembles *P. portoricensis* and *P. macdonaldi* Vaughan, 1919. It differs primarily in its thick coenosteal reticulum with small calices and generally mound-like shape. The pali are notably poorly-developed, and the septa are thin and heavily ornamented and extend to the columellar synapticular ring.

As shown in Text-figure 17, *P. waylandi* slightly resembles the modern Caribbean species *P. astreoides* Lamarck, 1816. It also resembles modern specimens with widely-spaced corallites of *P. branneri* Rathbun, 1887, and some specimens of the modern species *P. verrilli* Rehberg, 1883. However, in *P. waylandi,* the calices are notably shallower, and the columella tubercle better-developed than in the three modern species. The columellar synapticular ring is thick but narrow, and all 12 septa extend to it. Unlike *P. branneri,* calices of *P. waylandi* have only approximately four weak pali.

As shown on Text-figure 16a, *P. waylandi* is similar morphologically to at least three Miocene Mediterranean species of *Porites* (*P. calabricae* Chevalier, 1961, *P. pachysepta* Chevalier, 1961, and *P. maigensis* Kühn, 1925), which all have well-developed wall structures and coenosteal reticula. Of these three, *P. maigensis* most closely resembles *P. waylandi* in corallite diameter, septal arrangement, thinner synapticulae, and the reduced columellae and pali. *Porites maigensis,* however, typically forms branches and not mounds or plates as does *P. waylandi.*

Occurrence.—Río Cana: Cercado Formation (NMB locs. 16853, 16855, 16856), Gurabo Formation (NMB locs. 16817, 16819, 16823, 16881), and Mao Formation (NMB loc. 16885). Río Gurabo: Gurabo Formation (NMB locs. 15846, 15878, 15887, 16811, 16933) and Mao Formation (NMB loc. 15826). Río Yaque del Norte: Baitoa Formation (NMB locs. 16936, 16943, 17272, 17273, 17275, 17277, 17284, 17289).

Distribution.—*Porites waylandi* is widely distributed across the Caribbean from late Oligocene to early Pliocene time. The occurrences in the Dominican Republic are the youngest reported for the species. It has been found outside the Dominican Republic in the following strata: (1) Upper Oligocene La Quinta Formation of Chiapas, Mexico; (2) Lower Miocene Tampa Formation of Florida, Lares Formation of Puerto Rico, Río Lajas and Santa Ana formations of Chiapas, Mexico; and (3) Middle Miocene La Boca Formation of Panama, and Ponce Formation of Puerto Rico.

Genus **GONIOPORA** Blainville, 1830

Goniopora Blainville, 1830, pp. 359–360.

Type species.—*G. pendunculata* Quoy and Gaimard *in* Blainville, 1830. Recent. Port Dorey, New Guinea.

Diagnosis.—Colonies massive, ramose, or columnar, rarely encrusting. Corallites usually greater than 2.5 mm in diameter, separated by a distinctive, although poorly-developed coenosteal reticulum. Septa usually 24 in number, arranged in three cycles following a definite bilaterally-symmetric formula that consists of a dorsal and a ventral septum, two free secondary septa, and four lateral septal pairs (as described by Bernard, 1903). All secondary septa are joined on either side by a tertiary septum. Septa composed of four to eight trabeculae, the innermost of which may form pali when thickened. Columella trabecular, spongy, and well-developed.

Remarks.—The genus *Goniopora* occurs today only in the Indo-Pacific region and consists of 32 recognizable species (Veron and Pichon, 1982). It is especially abundant along the northern shores of Australia, through Indonesia into the South China Sea, and across the Indian Ocean into the Red Sea. Ecologically, *Goniopora* is abundant and known to occur in a broad range of reef habitats extending from the lagoon across the reef crest to the forereef slope.

The oldest known fossil representative of the genus is from the lower Cretaceous of Crimea. The genus was common in the Eocene, Oligocene, and Miocene of the Mediterranean and Caribbean, and in the Miocene of the Middle East and Indonesia. It apparently went extinct in the Mediterranean at the end of the Miocene during the Messinian salinity crisis and in the Caribbean during the early Pliocene (Bernard, 1903). Therefore, the occurrences in the Dominican Republic are among the youngest known for the genus in the Caribbean. Approximately 10 species names have been proposed for the Caribbean region during the Neogene.

Goniopora hilli Vaughan, 1919

Plate 32, figures 1–6; Plate 33, figures 1–6; Plate 34, figures 1–4; Plate 35, figures 1, 2; Text-figures 2, 3, 6, 8, 11, 13, 14

Goniopora hilli Vaughan, 1919, pp. 488–489, pl. 142, figs. 1, 1a.
Goniopora jacobiana Vaughan, 1919, pp. 492–493, pl. 144, figs. 1–3a.
Goniopora canalis Vaughan, 1919, pp. 494–495, pl. 146, figs. 1–2.
Goniopora aucillana Weisbord, 1973, pp. 30–32, pl. 33, fig. 1; pl. 34, fig. 1; pl. 35, fig. 1.
Goniopora tampaensis Weisbord, 1973, p. 36, pl. 15, figs. 1–2.

Description.—Colonies massive, hemispherical or encrusting; often large (19.6 cm in diameter). Colony surface smooth; may have slight irregularities. Growth bands pronounced, at 2- to 3-mm intervals. Calices polygonal, intermediate in size (2.6 to 3.1 mm), moderately deep (0.5 to 1.1 mm) with regular, narrow to intermediate spacing. Theca composed of three to five trabecular rows, 0.5 to 0.9 mm thick, crossed by low costae. Coenosteal reticulum narrow and smooth. Septa 23 to 27 in number, composed of three to five non-palar trabeculae that form prominent surface denticles. Primary and secondary septa of equal length and thickness (0.06 to 0.1 mm), extending without fusing to the outer palar synapticular ring. Tertiary septa well-developed, long (0.6 to 0.9 mm), fusing with the secondary septa. Pali weak, irregular, eight to 12 in number. Columella tangle narrow (0.7 to 1.2 mm in total diameter). Synapticulae thin, in six to seven rings. Septa slope gradually from the wall to the center of the columella tangle, forming a narrow, V-shaped fossa.

In thin-section, vertical trabeculae and horizontal septal junctions are equally thick and well-developed; forming abundant circular pores 0.2 to 0.3 mm in diameter, especially across the coenosteum and vertically along septal planes. Dissepiments are prominent, occurring at 0.5- to 1.5-mm intervals. Synapticulae are common, occurring at 0.4-mm intervals vertically up a corallite. The columella is formed by two to three twisted trabeculae, the septa by four to five trabeculae that curve gently toward the columella, and the theca by three to five irregular, incomplete trabecular rows. Corallites (especially their columellae) can be traced into the center of the corallum; but because the theca is highly porous and irregular and its texture is similar to that of the septa, the margins between corallites are commonly difficult to discern.

Holotype.—USNM 325058 (refigured here: Pl. 32, fig. 1; Pl. 33, fig. 1).

Measurements of the holotype.—Means of five corallites: **CD** 3.23, **CS** 3.26, **L1** 1.136, **L2** 1.040, **L3** 0.656, **NN** 6.6, **NS** 22.8, **F1** 0.0, **F2** 5.2, **DS** 3.4, **DW** 46.8, **PL** 10.8, **SR** 4.4, **WR** 4.2, **T1** 0.092, **T2** 0.084, **T3** 0.096, **SD** 0.132, **P1** 0.136, **P2** 0.136, **C1** 0.200, **C2** 0.112, **CW** 0.886, **SY** 0.110, **WT** 0.764, **CE** 0.230, **PE** 0.382, **SE** 0.401, **WE** 1.491, **CH** 12.2, **CT** 52.7.

Type locality.—USGS locality 6016, Empire Quarry, Emperador Limestone Member of the La Boca Formation, Panama. Middle Miocene.

Lectotype of canalis *(herein selected).*—USNM 72891 (refigured here: Pl. 33, fig. 3). Vaughan (1919, pp. 494–495) designated three cotypes for this species, one of which has been selected as the lectotype (Vaughan, 1919, pl. 146, fig. 3). The remaining two cotypes, USNM 325052 (Vaughan, 1919, pl. 146, figs. 1, 2), are selected as paralectotypes.

Type locality of canalis.—USGS locality 6016, Empire Quarry, Emperador Limestone Member of the La Boca Formation, Panama. Middle Miocene.

Material.—20 boxes of fragments from 12 localities, representing approximately 15 colonies. Eight specimens measured.

Remarks.—Vaughan (1919) described three species of *Goniopora* with corallite diameters of 3 to 4 mm and a thin coenosteal reticulum: (1) *hilli,* which forms plates and has three to four teeth per septum, (2) *jacobiana,* which forms hemispherical mounds and columns and has five to six teeth per septum, and (3) *canalis,* which forms branches and has six teeth per septum. All three species have poorly-developed pali and columellae and wall thicknesses of approximately 1 mm. The holotypes of *hilli* and *canalis* are both poorly-preserved, as is characteristic of much of the material from the Empire Quarry of the La Boca Formation in Panama. The holotype of *hilli* is a fragment (possibly only a portion of the upper growth band of a larger colony), and that of *canalis* is distorted by compression. Study of the Dominican Republic material (Text-figs. 11, 13) suggests that all three species belong in the same cluster and should therefore be synonymized. Text-figure 11b shows that a fourth species, *G. panamensis* Vaughan, 1919, is closely related to the first three; however, *G. panamensis* has a distinctive coenosteal reticulum that commonly forms ridges, which clearly distinguishes it from related forms.

Weisbord (1973) described two new species of *Goniopora* from the vicinity of Tampa, Florida that also have corallite diameters of 3 to 4 mm: (1) *aucillana* from the upper Oligocene Suwannee Limestone, which is distinguished by having a thin laminar wall surrounded by synapticulae that give it a perforate appearance, and (2) *tampaensis* from the lower Miocene Tampa Formation, which is distinguished by its small columella and prominent pali. The holotype and only specimen of *aucillana* (FSU AU-1a) is deposited in Weisbord's collection at Florida State University. The wall structure of this specimen closely resembles specimens of ?*G. decaturensis* Vaughan, 1919, a species that is questionably synonymized with *G. imperatoris* Vaughan, 1919. However, the comparatively large corallites and small columella of *aucillana* are more suggestive of *hilli,* indicating that the diagnostic laminar wall structure that developed in both *imperatoris* and *hilli* may be a response to the environment. As shown by canonical discriminant analysis (Text-figs. 11, 13), the holotype and only specimen of *tampaensis* clearly falls within the *hilli* Dominican Republic cluster.

Rhodaraea irregularis Duncan, 1863 (p. 426), from the upper Oligocene of Antigua is a species of *Goniopora* with a colony shape and corallite diameters

similar to the Dominican Republic *hilli* cluster, yet it nevertheless differs in wall and septal structure. The species is based on only one worn, totally-silicified specimen whose septa are thinner and more numerous, walls more distinct, corallites more closely-spaced, and pali better-developed than those of the NMB Dominican Republic material. Therefore, it should be considered a separate species until more material from Antigua can be studied.

Re-examination of the Tertiary Puerto Rican corals described by Coryell and Ohlsen (1929) shows that specimens of four described species belong to *G. hilli*: AMNH 23051 (*G. jacobiana*) and AMNH 23048 (*G. hilli*) from Guanica, and AMNH 23052 (*G. panamensis* Vaughan, 1919) and AMNH 23039 (*G. canalis*) from the Lares Limestone.

Frost and Langenheim (1974) described six specimens of *G. hilli* from the upper Oligocene La Quinta Formation of Chiapas, Mexico, including two figured specimens. These specimens were originally deposited at the University of Illinois but have been lost (R. L. Langenheim, Jr., written commun., 1984). The photographs and description of this material, however, closely match the Dominican Republic specimens.

Variability.—Although morphologic variation within this species is not particularly extensive, *G. hilli* shows the most distinctive directional morphologic trends upsection of all the Poritidae studied. Comparisons between material from the Río Yaque del Norte section and from the Río Gurabo and Río Cana sections suggest that it increases its corallite diameter and its colony height significantly, possibly in response to increased water depth. Similarly, the amount of coenosteal reticulum and the thickness of the columella tangle may increase slightly upsection. Increases in corallite diameter, wall thickness, and columella thickness and a decrease in calice elevation can also be traced down the side of a colony.

Comparison.—*Goniopora hilli* overlaps slightly in morphology with *G. imperatoris,* so that intermediates occur occasionally between the two species clusters. The most important distinguishing characteristics of *G. hilli* are: (1) its larger corallite diameters; (2) its more elevated calices with reduced columella tangles; (3) its thinner, more irregular wall; and (4) its less distinctive coenosteal reticulum.

Of the five Neogene Mediterranean species of *Goniopora* described by Chevalier (1961), only one, *G. turonensis* Chevalier, 1961, is at all similar to *G. hilli.* However, its corallite diameter is smaller, and it forms only small spherical colonies.

Occurrence.—Río Cana: Gurabo Formation (NMB loc. 16818). Río Gurabo: Gurabo Formation (NMB locs. 15808, 15837, 15861, 15884, 16921, 16933). Río Yaque del Norte: Baitoa Formation (NMB locs. 16937, 16943, 16944, 17283, 17284).

Distribution.—*Goniopora hilli* ranges in age from late Oligocene to late Pliocene and has been found widely distributed across the northern and central Caribbean. It occurs outside of the Dominican Republic in the following strata: (1) Upper Oligocene Suwannee Limestone of Florida and ?La Quinta Formation of Chiapas, Mexico; (2) Lower Miocene Tampa Formation of Florida, Anguilla Formation of Anguilla, and Lares Formation of Puerto Rico; (3) Middle Miocene La Boca Formation of Panama, Chipola Formation of Florida, and Ponce Formation of Puerto Rico; and (4) Upper Pliocene La Cruz Marl of Cuba.

Goniopora imperatoris Vaughan

Plate 35, figures 3–7; Plate 36, figures 1–7; Plate 37, figures 1–4; Text-figures 2, 3, 6, 8, 11, 13, 14

not *Madrepora daedalea* Forskål, 1775, p. 133.
?*Alveopora daedalaea* var. *regularis* Duncan, 1863, p. 426, pl. 14, figs. 4a–c.
?*Goniopora decaturensis* Vaughan, 1919, pp. 490–491, pl. 143, figs. 1, 1a.
?*Goniopora decaturensis* var. *silicensis* Vaughan, 1919, p. 491, pl. 143, figs. 2, 2a.
?*Goniopora decaturensis* var. *bainbridgensis* Vaughan, 1919, p. 491, pl. 143, figs. 3, 3a.
Goniopora imperatoris Vaughan, 1919, pp. 493–494, pl. 142, figs. 3, 3a.

Description.—Colonies massive, columnar, hemispherical or plate-shaped; often large (>15 cm in diameter), but may form small irregular nodules, 5 cm in diameter. Colony surface smooth. Growth bands, pronounced, at 3- to 4-mm intervals. Calices circular, small (1.8 to 2.8 mm in diameter), shallow (0.3 to 1.1 mm in depth) with regular, intermediate spacing. Theca composed of three to five trabecular rows, crossed by weak costae. Coenosteal reticulum well-developed, with a smooth upper surface. Septa 20 to 29 in number, composed of three to five non-palar trabeculae that form weak surface denticles. Primary and secondary septa of equal length and thickness (0.06 to 0.10 mm), extending without fusing to the outer palar synapticular ring. Tertiary septa well-developed, of intermediate length (0.4 to 0.6 mm) fusing with the secondary septa. Pali well-developed, nine to 12 in number. Columella tangle relatively thick, 0.7 to 0.9 mm in total diameter. Synapticulae thin, in four to seven rings. Fossa U-shaped, extending one-half to two-thirds of the distance across the corallite.

In thin-section, horizontal septal junctions occur more frequently than vertical trabeculae. Trabeculae are thicker than septal junctions, although both are relatively thin. Circular pores (0.1 to 0.2 mm in diameter) are abundant, especially across vertical septal planes. Dissepiments are prominent, occurring at 0.7-

to 1.2-mm intervals. Synapticulae are common but poorly developed, occurring at 0.3-mm intervals vertically up the corallite. The columella is composed of two to three twisted trabeculae, the septa by three to four trabeculae that gently curve toward the columella, and the theca by five or more irregular, incomplete trabecular rows that commonly form a spongy coenosteal reticulum. Corallites can be traced to the center of the corallum. The thecal margin itself is relatively distinct and complete.

Holotype.—USNM 325049 (refigured here: Pl. 35, fig. 5; Pl. 36, fig. 7).

Measurements of the holotype.—Means of five corallites: **CD** 2.26, **CS** 2.80, **L1** 0.840, **L2** 0.660, **L3** 0.476, **NN** 6.4, **NS** 23.2, **F1** 1.6, **F2** 5.8, **DS** 4.0, **DW** 32.4, **PL** 8.8, **SR** 5.2, **WR** 3.8, **T1** 0.088, **T2** 0.072, **T3** 0.072, **SD** 0.116, **P1** 0.096, **P2** 0.140, **C1** 0.188, **C2** 0.080, **CW** 0.818, **SY** 0.086, **WT** 0.760, **CE** 0.287, **PE** 0.306, **SE** 0.344, **WE** 0.650, **CH** 54.1, **CT** 49.2.

Type locality.—USGS locality 6016, Empire Quarry, Emperador Limestone Member of the La Boca Formation, Panama. Middle Miocene.

Material.—18 boxes of fragments from eight localities, representing approximately 13 colonies. Seven specimens measured.

Remarks.—Vaughan (1919) described two new species of massive *Goniopora* from the Caribbean Neogene with corallite diameters of 1.5 to 3 mm and well-developed columellae: (1) *decaturensis,* which forms plates and has a membraniform wall structure and (2) *imperatoris,* which forms lobate columns and has a well-developed coenosteal reticulum. In addition, two varieties of *decaturensis* are described: one with larger corallites (2.5 to 4 mm) named var. *silicensis*; and the other forming small, rounded masses named var. *bainbridgensis.* Study of the Dominican Republic material (Text-fig. 11) suggests that the two species are very similar, with the Dominican Republic material more closely resembling *imperatoris.* Nevertheless, the significance of the membraniform wall structure in *decaturensis* remains unclear without study of additional material from the Chattahoochee Formation of Decatur County, Georgia. Therefore, *decaturensis* is only questionably synonymized. Because of their larger corallites, the two varieties appear almost intermediate between *imperatoris* and *hilli,* although their thicker, more delicate intercorallite reticulum is more indicative of *imperatoris.*

Duncan (1863) described two new varieties and one new species of *Goniopora* from the Oligocene of Antigua with corallite diameters of 1.25 to 2.5 mm: (1) *Alveopora daedalaea* var. *regularis* with larger corallites and a coenosteal reticulum; and (2) *Alveopora daedalaea* var. *minor* Duncan, 1863, and (3) *Alveopora microscopica* Duncan, 1863, both with smaller calices and a lamellate wall structure. All three types are completely silicified and thus poorly-preserved. Varieties *minor* and *microscopica* have almost identical corallite morphologies. They differ from *imperatoris* in their more solid, straight walls that lack coenosteal reticulum, and on further examination of additional material these varieties may prove to represent a distinct species. On the other hand, var. *regularis* appears very close to *imperatoris*; however, because of the poor preservation of the type material, it is only questionably synonymized.

In Vaughan's collections at the USNM, there is a specimen (USNM 63251) from the Baitoa Formation of the Río Yaque del Norte of the Dominican Republic (USGS loc. 8668), which clearly falls in the *imperatoris* cluster as defined herein. Vaughan identified this coral as *Goniopora calhounensis,* a name which he never formally described, even in an unpublished manuscript. Later, Weisbord (1971) used the name in describing another species of *Goniopora* from the Chipola Formation of Florida. Weisbord's species is described later in this paper.

In the middle Miocene Ponce Formation collections described by Coryell and Ohlsen (1929), specimens of four species belong to *G. imperatoris* as currently defined: (1) AMNH 23049, *Goniopora imperatoris*; (2) AMNH 23044, *Goniopora decaturensis,* and AMNH 23046, *Goniopora decaturensis silicensis*; (3) AMNH 23056, *Goniopora regularis*; (4) AMNH 23048, *Goniopora hilli*; and (5) AMNH 23082, *Porites panamensis* Vaughan, 1919. These specimens have generally thinner coenosteal reticula, sometimes forming straight, lamellar wall ridges between calices. These morphologic differences may represent a response to shallower, less turbid marine conditions.

Study of Frost and Langenheim's (1974) specimens of *Goniopora imperatoris* from the lower Miocene Santa Ana Formation of Chiapas, Mexico (UI X3606, X3607) reconfirms that they belong to *G. imperatoris.* Their specimen of *Goniopora regularis* from the upper Oligocene La Quinta Formation of Chiapas (UI X3538) has been lost; however, the photographs (pl. 80, figs. 4–7) and description (pp. 234–236) closely resemble an *imperatoris* with reduced coenosteal reticulum.

Variability.—Study of the Dominican Republic *G. imperatoris* shows that variability is reduced in this species. The canonical variable cluster is relatively tight (Text-fig. 11), and low standard deviations were found in single characters (Text-fig. 15, Appendix Ib). Significant unidirectional trends can only be detected upsection in colony shape, which shows a slight increase

(Text-fig. 6). Subjective examination of within-colony variability shows that corallites become slightly smaller and the wall thinner from colony top to side.

Comparison.—*Goniopora imperatoris* overlaps slightly with *G. hilli* as discussed in the *Comparison* section for *G. hilli*. However, it resembles no other Neogene Caribbean or Mediterranean species. It is similar morphologically to *G. microscopica* (Duncan, 1863), from the Oligocene of Antigua, as described above in *Remarks*.

Two Eocene species of *Goniopora* from the Caribbean that are close to *G. imperatoris* include *G. taberi* Wells, 1934 and *G. copoyensis* Frost and Langenheim, 1974. *Goniopora taberi* differs from *G. imperatoris* by having a ramose growth form and styliform columella. *Goniopora copoyensis* has a similar well-developed coenosteal reticulum; however, its corallites have notably smaller diameters (1.2 to 1.5 mm) and fewer septa than are characteristic of *G. imperatoris*.

Occurrence.—Río Cana: Cercado Formation (NMB locs. 16853, 16856), Gurabo Formation (NMB loc. 16818), and Mao Formation (NMB loc. 16876). Río Mao: ?Gurabo Formation (NMB loc. 16911). Río Yaque del Norte: Baitoa Formation (NMB locs. 16939, 16944, 17284).

Distribution.—*Goniopora imperatoris* ranges in age from early Miocene (possibly late Oligocene) to early Pliocene and has been found widely distributed across the central and possibly northern Caribbean. The occurrences in the Dominican Republic are the youngest reported for the species. It has been found outside the Dominican Republic in the following strata: (1) Upper Oligocene ?Antigua Formation of Antigua and ?La Quinta Formation of Chiapas, Mexico; (2) Lower Miocene Anguilla Formation of Anguilla and ?Chattahoochee Formation of Georgia; and (3) Middle Miocene La Boca Formation of Panama and Ponce Formation of Puerto Rico.

Goniopora calhounensis Weisbord

Plate 38, figures 1–3; Text-figures 11, 15, 16

Goniopora calhounensis Weisbord, 1971, pp. 18–20, pl. 4, figs. 5, 6.

Description.—Colonies massive, hemispherical, large (10 cm in maximum diameter). Colony surface smooth. Calices polygonal, large (3.8 to 5 mm in diameter), shallow (0.65 to 0.75 mm in depth) with regular, wide spacing. Theca composed of four to five trabecular rows, 1 mm thick. Coenosteal reticulum well-developed, with a smooth upper surface. Septa 26 to 27 in number, composed of four to five non-palar trabeculae that form prominent surface denticles. Primary and secondary septa of equal length and thickness (0.14 to 0.2 mm) extending without fusing to the outer palar synapticular ring. Tertiary septa, well-developed, long (1.1 to 1.4 mm) fusing with the secondary septa. Pali well-developed, 12 to 13 in number. Columella tangle relatively thick (1.3 to 1.4 mm in total diameter). Synapticulae moderately thick (0.11 to 0.16 mm) in six to eight rings. Septa slope gradually from the wall to the center of the columella tangle, forming a narrow V-shaped fossa.

Holotype.—FSU CH3-3a, Weisbord collection, Department of Geology, Florida State University, Tallahassee, Florida (refigured here: Pl. 38, fig. 1).

Measurements of the holotype.—Means of five corallites: **CD** 4.91, **CS** 6.57, **L1** 1.42, **L2** 1.31, **L3** 1.24, **NN** 7.2, **NS** 25.6, **F1** 0.0, **F2** 3.6, **DS** 6.4, **DW** 50.0, **PL** 16.4, **SR** 7.0, **WR** 6.2, **T1** 0.13, **T2** 0.10, **T3** 0.12, **SD** 0.24, **P1** 0.20, **P2** 0.21, **C1** 0.22, **C2** 0.14, **CW** 2.42, **SY** 0.14, **WT** 1.47, **CE** 0.24, **PE** 0.24, **SE** 0.44, **WE** 0.70, **CH** 9.1, **CT** 27.0.

Type locality.—Tenmile Creek, one mile southeast of bridge on state road 73, Calhoun County, Florida. Chipola Formation, Lower Miocene.

Material.—Two colonies from two localities. Two specimens measured.

Remarks.—Weisbord (1971) originally described this species as consisting of fragments in the Florida State University collection and a few specimens at the USNM and the ANSP. The specimens at the USNM bearing Vaughan's label "*Goniopora calhounensis*" clearly belong to *G. imperatoris* as discussed earlier in the *Remarks* section for that species. The ANSP specimen (ANSP 10933), which Weisbord described as typical of *G. calhounensis*, belongs instead to *Goniopora hilli*. I have been unable to locate any other material. This leaves only three specimens (the holotype and the two NMB Dominican Republic specimens) that actually belong to the species.

Variability.—Because of the poor preservation and scarcity of material, it is difficult to assess variability within this species. Wide variability has been noted in corallite diameter, septum length, and total number of septa (Text-fig. 15); however, subjective examination of these characters shows no distinctive trends that can be related to environment. Therefore, variation in size-related characters may be caused by ontogeny. Little variation is noted in wall thickness or the coenosteal reticulum (Text-fig. 15).

Comparison.—*Goniopora calhounensis* is markedly distinct from all other Tertiary Caribbean *Goniopora* including *G. hilli* Vaughan, 1919, and *G. imperatoris* Vaughan, 1919, because of its large, flat corallites with well-developed columella tangles. As shown in Text-figure 11, no overlap is found with the first two *Go-*

niopora species. Two species described by Chevalier (1961) from the Burdigalian of the Aquitaine Basin (St. Paul-les-Dax, France), however, closely resemble *G. calhounensis* in these characters: (1) "*Goniopora daxitertia* Bernard" and (2) *Goniopora globulosa* Chevalier, 1961. The only distinctive difference between *calhounensis* and these two Mediterranean species is in wall structure which appears to be wider, less porous, and better-developed in *G. calhounensis.*

Occurrence.—Río Cana: Mao Formation (NMB loc. 16875). Río Gurabo: Gurabo Formation (NMB loc. 16921).

Distribution.—*G. calhounensis* appears to be restricted to the Miocene and lower Pliocene of the northeast Caribbean. The only occurrence outside the Dominican Republic is in the lower Miocene Chipola Formation of Florida.

Genus **ALVEOPORA** Blainville, 1830

Alveopora Blainville, 1830, pp. 358–359.

Type species.—*Madrepora daedalea* Forskål, 1775. Recent. Red Sea. The holotype of this species has been lost and there is some doubt as to whether it actually belongs to the genus *Alveopora* as now conceived by many coral workers (see Veron and Pichon, 1982).

Diagnosis.—Colonies massive or ramose. Corallites circular or polygonal, mostly juxtaposed. Septa usually 12 in number, having no regular pattern of fusion, and composed of spines that project inward from the theca. Vertical septal trabeculae rarely developed. Theca composed of 12 trabeculae linked by horizontal synapticulae to form a lattice-like arrangement of pores.

Remarks.—The genus *Alveopora* occurs today only in the Indo-Pacific region and consists of approximately 15 described species (Veron and Pichon, 1982). It has been recorded from as far east as Hawaii and Samoa across Micronesia and Indonesia through the Maldives to the Red Sea. Veron and Pichon (1982) have recognized seven species in eastern Australia. Ecologically, *Alveopora* occurs in a range of reef habitats; however, it is seldom abundant, and species distributions are usually narrowly confined.

The oldest known fossil representative of the genus is from the Eocene of Madagascar. The genus is well-known in Europe during the Oligocene and Miocene but it occurs only rarely in the Caribbean during the Oligocene, Miocene, and Pliocene. Only two names, *Alveopora chiapanecae* Frost and Langenheim, 1974 and *Alveopora tampae* Weisbord, 1973, have been proposed for the Caribbean region during the Tertiary.

Alveopora tampae Weisbord
Plate 38, figures 4–7

Alveopora tampae Weisbord, 1973, pp. 37–38, pl. 6, figs. 4–6, pl. 7, figs. 4–5.

Description.—Colonies massive with even surfaces, usually forming small regular spheres less than 4 cm in diameter. Calices circular, 2 to 3 mm in diameter. Septal spines arranged in two complete cycles with an occasional incomplete third cycle. Theca thick (0.5 mm), composed of one to three trabeculae. Endothecal dissepiments 0.2 mm thick, spaced at 0.8- to 1.2-mm intervals. Thecal pores equal, regularly arranged, circular (some elongate), approximately 0.5 mm in diameter, separated by synapticulae approximately 0.2 to 0.3 mm thick.

Holotype.—The holotype cannot be found at the USNM. Its catalog number was incorrectly cited by Weisbord (1973) as USGS 2115, which is a locality number. Two topotypes (USNM 66224, 66225) were therefore studied and are figured here on Plate 38, figures 4–6.

Measurements of a topotype (USNM 66224).—Means of five corallites: **CD** 2.42, **CS** 3.18, **L1** 0.96, **L2** 0.29, **NN** 6.4, **NS** 12.6, **WR** 1.5, **T1** 0.20, **T2** 0.13, **SY** 0.19, **WT** 0.625, **CH** 28.2, **CT** 31.9.

Type locality.—USGS 2115, 2.5 miles west of Tampa, Florida along the shores of Hillsborough Bay, Tampa Formation. Lower Miocene.

Material.—One colony from one locality, deposited at the USNM.

Appendix Ia.—Means (±1 standard deviation) of all corallite characters in the five species of *Porites* herein described. Abbreviations for characters are explained in Table 3. "n" = number of colonies measured. Five corallites were measured in each colony.

	P. convivatoris (n = 10)	*P. baracoaensis* (n = 32)	*P. macdonaldi* (n = 15)	*P. waylandi* (n = 15)	*P. portoricensis* (n = 30)
CD*	1.37 (±0.17)	1.24 (±0.17)	1.45 (±0.23)	1.42 (±0.15)	1.69 (±0.28)
CS	1.33 (±0.14)	1.32 (±0.17)	1.81 (±0.26)	1.84 (±0.26)	1.98 (±0.24)
L1*	0.410 (±0.059)	0.398 (±0.082)	0.404 (±0.088)	0.440 (±0.080)	0.554 (±0.094)
L2	0.506 (±0.068)	0.489 (±0.070)	0.493 (±0.083)	0.498 (±0.077)	0.607 (±0.122)
L3	0.521 (±0.080)	0.494 (±0.077)	0.474 (±0.065)	0.523 (±0.091)	0.612 (±0.109)
NN	6.5 (±0.4)	6.5 (±0.4)	7.0 (±0.4)	7.4 (±0.6)	6.6 (±0.3)
NS	12.0 (±0.1)	12.0 (±0.2)	11.8 (±0.4)	12.0 (±0.4)	12.0 (±0.2)
NB	2.2 (±1.2)	4.1 (±1.7)	1.9 (±0.6)	2.0 (±0.5)	2.3 (±1.0)
DS†	2.0 (±0.4)	2.3 (±0.4)	2.3 (±0.4)	2.9 (±0.5)	2.8 (±0.5)
DW	25.3 (±2.7)	25.9 (±2.8)	19.5 (±1.7)	22.0 (±2.5)	24.1 (±1.5)
PL*	4.3 (±0.5)	5.0 (±0.5)	4.0 (±1.1)	3.5 (±1.1)	3.3 (±0.7)
SR†	2.0 (±0.2)	2.8 (±0.4)	3.0 (±0.4)	3.4 (±0.4)	3.4 (±0.4)
WR*	1.6 (±0.5)	1.2 (±0.2)	3.1 (±0.5)	3.5 (±0.7)	3.0 (±0.7)
T1	0.090 (±0.015)	0.098 (±0.012)	0.106 (±0.020)	0.092 (±0.015)	0.116 (±0.025)
T2	0.091 (±0.021)	0.106 (±0.014)	0.112 (±0.020)	0.094 (±0.010)	0.126 (±0.030)
T3	0.098 (±0.021)	0.106 (±0.012)	0.106 (±0.016)	0.096 (±0.012)	0.122 (±0.025)
SD†	0.105 (±0.014)	0.125 (±0.021)	0.130 (±0.056)	0.116 (±0.015)	0.130 (±0.023)
P1	0.002 (±0.005)	0.014 (±0.020)	0.021 (±0.020)	0.019 (±0.021)	0.013 (±0.023)
P2	0.087 (±0.023)	0.114 (±0.027)	0.089 (±0.053)	0.050 (±0.037)	0.053 (±0.043)
P3	0.093 (±0.022)	0.111 (±0.016)	0.111 (±0.027)	0.093 (±0.019)	0.101 (±0.029)
C1	0.122 (±0.059)	0.071 (±0.037)	0.177 (±0.052)	0.144 (±0.049)	0.138 (±0.040)
C2	0.079 (±0.035)	0.059 (±0.031)	0.199 (±0.033)	0.097 (±0.034)	0.103 (±0.030)
CW*	0.416 (±0.055)	0.427 (±0.053)	0.599 (±0.067)	0.507 (±0.040)	0.555 (±0.080)
SY†	0.085 (±0.018)	0.113 (±0.020)	0.114 (±0.015)	0.094 (±0.012)	0.124 (±0.023)
WT*	0.170 (±0.075)	0.120 (±0.030)	0.602 (±0.124)	0.652 (±0.156)	0.508 (±0.158)
CE	0.22 (±0.06)	0.14 (±0.08)	0.26 (±0.08)	0.22 (±0.10)	0.21 (±0.06)
PE	0.46 (±0.11)	0.37 (±0.41)	0.32 (±0.09)	0.33 (±0.08)	0.31 (±0.08)
SE	0.53 (±0.08)	0.35 (±0.07)	0.36 (±0.10)	0.37 (±0.06)	0.43 (±0.10)
WE*	0.79 (±0.12)	0.43 (±0.08)	0.65 (±0.12)	0.71 (±0.15)	0.69 (±0.17)

* characters whose means and standard deviations are diagrammed in Text-figure 14.
† characters not used in canonical discriminant analyses.

Appendix Ib.—Means (±1 standard deviation) of all corallite characters in the three species of *Goniopora* herein described. Abbreviations for characters are explained in Table 4. "n" = number of colonies measured. Five corallites were measured in each colony.

	G. imperatoris (n = 10)	*G. hilli* (n = 6)	*G. calhounensis* (n = 2)		*G. imperatoris* (n = 10)	*G. hilli* (n = 6)	*G. calhounensis* (n = 2)
CD*	2.19 (±0.30)	2.92 (±0.19)	4.44 (±0.79)	**T2†**	0.076 (±0.011)	0.082 (±0.015)	0.174 (±0.042)
CS	2.49 (±0.22)	3.04 (±0.30)	4.37 (±0.66)	**T3†**	0.064 (±0.010)	0.073 (±0.015)	0.160 (±0.023)
L1*	0.734 (±0.106)	1.005 (±0.085)	1.646 (±0.320)	**SD†**	0.109 (±0.013)	0.139 (±0.028)	0.248 (±0.028)
L2	0.624 (±0.076)	0.915 (±0.056)	1.370 (±0.167)	**P1**	0.090 (±0.017)	0.112 (±0.014)	0.154 (±0.048)
L3	0.497 (±0.064)	0.771 (±0.094)	1.272 (±0.215)	**P2**	0.139 (±0.040)	0.137 (±0.037)	0.208 (±0.040)
NN	6.5 (±0.3)	6.5 (±0.2)	6.8 (±0.3)	**C1**	0.167 (±0.047)	0.186 (±0.058)	0.212 (±0.006)
NS*	23.7 (±2.1)	24.3 (±1.5)	26.4 (±1.1)	**C2**	0.088 (±0.023)	0.125 (±0.028)	0.160 (±0.034)
F1†	0.8 (±1.9)	0.6 (±0.4)	0.0 (±0.0)	**CW***	0.871 (±0.095)	0.929 (±0.166)	1.350 (±0.062)
F2†	5.6 (±0.3)	5.6 (±0.2)	5.4 (±0.3)	**SY***	0.077 (±0.007)	0.084 (±0.014)	0.139 (±0.024)
DS†	4.3 (±0.6)	5.3 (±0.7)	5.8 (±0.6)	**WT***	0.647 (±0.093)	0.688 (±0.153)	1.050 (±0.008)
DW	33.0 (±3.5)	38.4 (±3.5)	45.3 (±5.8)	**CE**	0.23 (±0.07)	0.26 (±0.05)	0.27 (±0.03)
PL*	10.7 (±0.9)	9.8 (±1.5)	12.2 (±0.6)	**PE**	0.31 (±0.10)	0.32 (±0.07)	0.26 (±0.01)
SR	5.7 (±0.6)	6.9 (±0.6)	7.2 (±1.1)	**SE***	0.25 (±0.10)	0.40 (±0.12)	0.29 (±0.05)
WR	3.8 (±0.4)	3.8 (±0.6)	4.5 (±0.4)	**WE**	0.66 (±0.23)	0.76 (±0.22)	0.71 (±0.05)
T1†	0.077 (±0.016)	0.091 (±0.020)	0.172 (±0.040)				

* characters whose means and standard deviations are diagrammed in Text-figure 15.
† characters not used in canonical discriminant analyses.

Appendix IIa.—Canonical discriminant analysis of *Porites* groups 2 and 4. Total-sample correlations between the canonical variable and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. Abbreviations for characters are explained in Table 3.

	COR	SCC
NS	—	−0.83
PL	0.534	0.80
WR	−0.546	−1.53
T2	—	0.96
T3	—	−1.34
C1	—	−1.76*
C2	—	0.98
SE	−0.740	—
WE	−0.910*	−1.57

Appendix IIc.—Canonical discriminant analysis of *Goniopora* groups 1 and 2. Total-sample correlations between the canonical variable and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. Abbreviations for characters are explained in Table 4.

Original variable	COR	SCC
CD	0.802*	1.04*
CS	0.640	0.68
L1	0.705	—
L2	0.793*	—
L3	0.800*	0.49
NN	—	−0.53
DW	0.517	—
SR	0.596	—
CE	—	0.56

Appendix IIb.—Canonical discriminant analysis of *Porites* groups 1, 3, and 5. Total-sample correlations between the canonical variables and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. The canonical variables are labelled CV1–2. Abbreviations for characters are explained in Table 3.

Original variable	CV1		CV2	
	COR	SCC	COR	SCC
CD	−0.458	0.80	—	—
CS	—	−1.03	—	—
L1	−0.656*	−2.08*	—	—
L2	−0.490	0.93	—	—
L3	−0.592	−0.79	—	0.45
NN	0.427	—	0.614*	0.72
WR	—	−0.71	—	0.48
T1	—	—	−0.452	—
T2	—	—	−0.513	—
T3	—	—	−0.438	—
CW	—	1.28	−0.516	−1.13*
WT	—	0.94	—	—
PE	—	—	—	0.59
SE	—	—	—	−0.99
WE	—	—	—	0.83

Appendix IId.—Canonical discriminant analysis of five fossil and six modern Caribbean species of *Porites*. Total sample correlations between the canonical variables and the original variables (COR), and standardized canonical coefficients (SCC). Only values with high magnitudes are given. The canonical variables are labelled CV1–5. Abbreviations for characters are explained in Table 3.

Original variable	CV1		CV2		CV3		CV4		CV5	
	COR	SCC	COR	SCC	COR	SCC	COR	SCC	COR	SCC
CD	—	0.72	—	—	—	—	—	—	—	—
CS	0.702	—	—	0.68	—	—	—	0.55	—	—
L1	—	—	0.502*	0.60	—	−0.94	—	—	—	—
L2	—	—	—	—	—	—	—	−0.61	0.485*	—
L3	—	—	—	—	−0.360	—	—	—	—	—
NN	—	—	—	—	—	—	0.484	0.65	—	—
NB	−0.586	—	—	—	—	—	—	0.45	—	—
DW	−0.516	−0.71	—	0.76	−0.376	—	—	—	—	—
PL	−0.522	—	—	—	—	—	—	—		—
WR	0.857*	1.14*	—	0.69	—	−1.30*	—	—	—	1.10
T2	—	—	0.456	—	—	—	—	0.64	0.424	—
T3	—	—	0.463	—	—	—	—	—	0.487*	—
P2	−0.536	—	—	—	—	—	—	—	0.410	—
P3	—	—	—	—	—	—	—	—	0.481*	—
C1	0.593	—	—	—	—	—	—	−0.63	—	—
CW	0.617	—	—	—	—	0.83	—	−0.47	—	—
WT	0.866*	0.51	—	—	—	1.25	—	0.69	—	−1.81*
CE	—	—	—	—	—	0.83	−0.534*	—	—	—
SE	—	—	−0.519*	−0.58	−0.404*	—	—	−0.84*	—	—
WE	0.614	1.02	−0.480	−1.12*	−0.377	−0.98	—	0.67	—	—

* most important variables.

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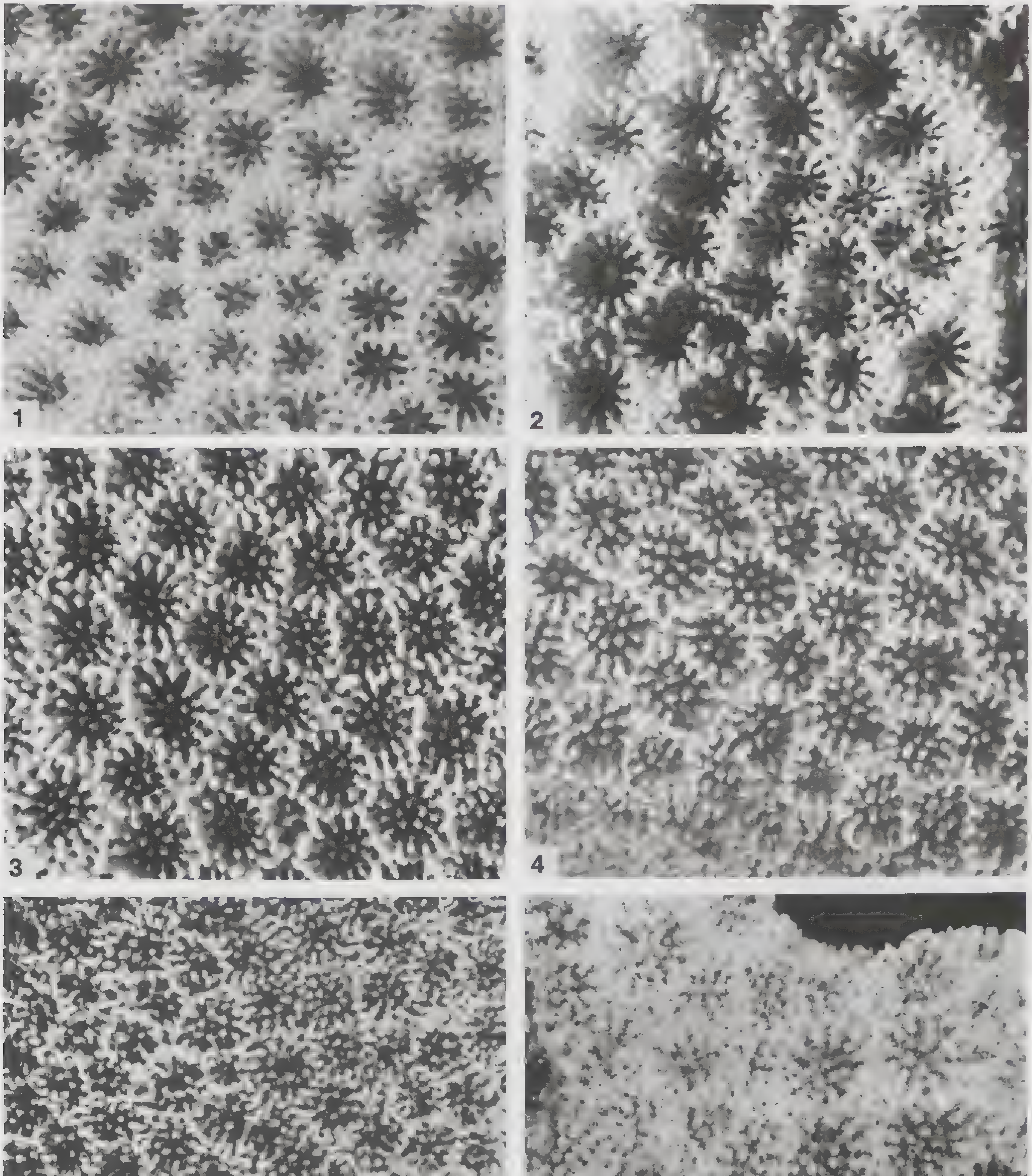
EXPLANATION OF PLATE 15

Page

Calices of six modern described species of *Porites* from the Caribbean/Western Atlantic region 56
All photos, ×10. The three massive species (figs. 1–3) have traditionally been distinguished on the basis of calice characters such as wall thickness, calice elevation, development of pali, and development of the columella tubercle. The three branched species (figs. 4–6) have been distinguished on the basis of branch thickness: *P. porites* with swollen branch tips, greater than 20 mm in diameter; *P. furcata* with dichotomous branching, about 10 mm in diameter; *P. divaricata* with thin branches, less than 6 mm in diameter. Vaughan (1901) believed only two true species existed in the Caribbean: one represented by figures 1 and 2, the other by figures 3 through 6; whereas, more recent studies such as Brakel (1976, 1977) and Wells and Lang (1973) suggest that there may be as many as four to six. Calices of the Neogene Dominican Republic *Porites* clearly differ from these modern specimens by having generally larger, shallower corallites. Calices of *P. porites* (Pallas) in figure 4 and *P. divaricata* Lesueur in figure 6 slightly resemble one of the fossil species, *P. convivatoris* (Text-fig. 15).

Figure

1. ***Porites astreoides*** Lamarck, 1816.
   Holotype. MHNP, Lamarck Collection No. 169, Mers d'Amérique; distinguished by deep calices, the lack of pali, and a small columella tubercle.
2. ***Porites verrilli*** Rehberg, 1893.
   Holotype. YPM 4539, Abrolhos Reefs, Brazil; like *P. astreoides* but having extensive coenosteal reticulum, deeper calices, and a prominent columella tubercle.
3. ***Porites branneri*** Rathbun, 1887.
   Holotype. USNM 10961, Parahyba do Norte, Brazil; distinguished by a prominent circle of five pali and no columella tubercle.
4. ***Porites porites*** (Pallas, 1766).
   Figured Specimen. MHNP, Lamarck Collection No. 150, Antilles (holotype of *Porites clavaria* Lamarck); distinguished by shallow, large calices with six pali and a columella tubercle.
5. ***Porites furcata*** var. 2 of Lamarck, 1816.
   Figured Specimen. MHNP, Lamarck Collection No. 155, Mers d'Amérique; like *P. branneri* but having smaller calices.
6. ***Porites divaricata*** Lesueur, 1821.
   Figured Specimen. USNM 72377, East of Pulaski Buoy, Florida; like *P. porites* but having shallower calices.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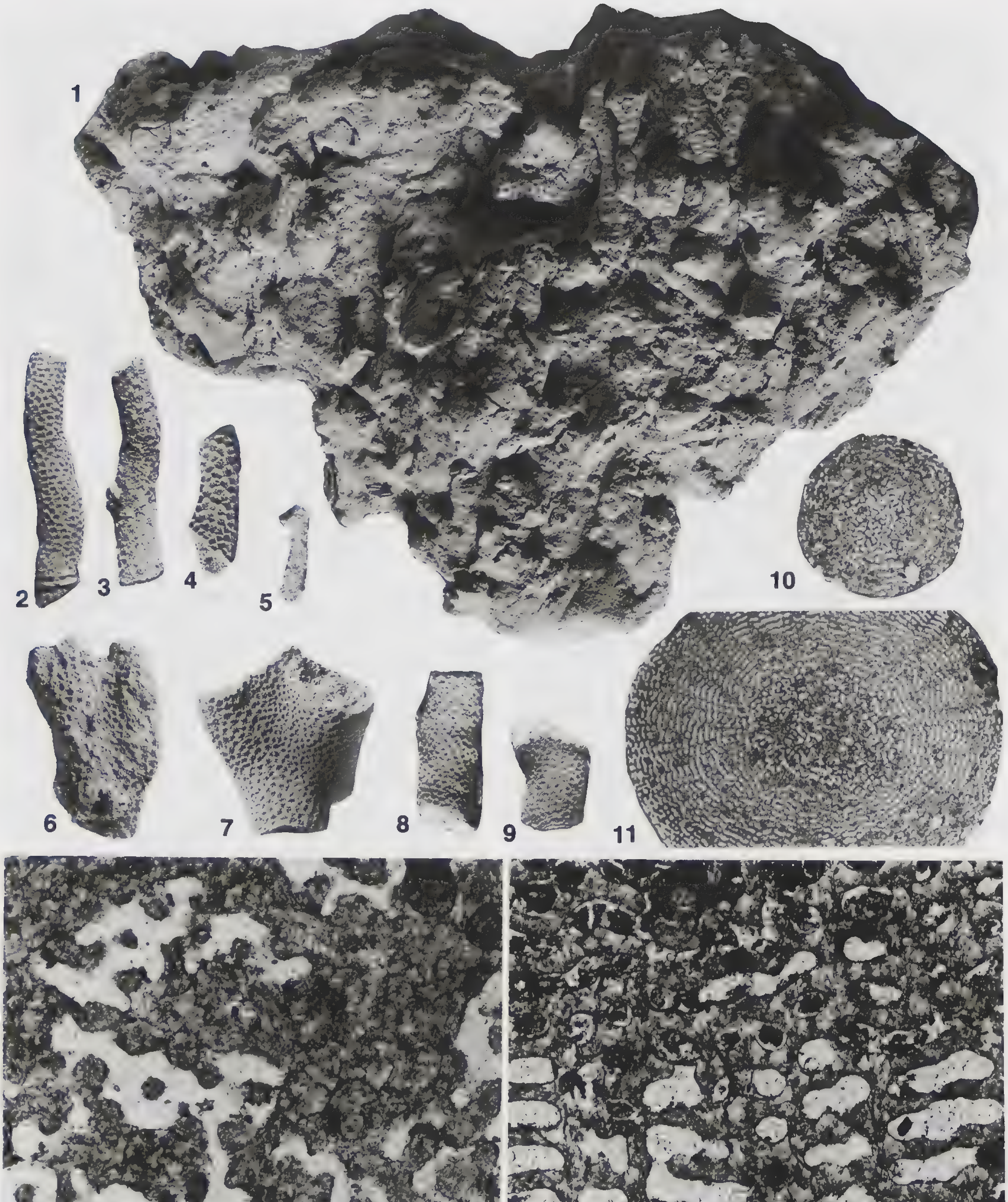
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EXPLANATION OF PLATE 16

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Porites baracoaensis Vaughan 75

Branch fragments and thin-sections. The colony morphology is fairly uniform, forming bushes with branches commonly 0.5 to 1.5 cm in thickness. In thin-sections cut perpendicular to branch axes, an irregular core is seen surrounded by a uniform network of horizontal septal junctions and vertical trabeculae. The vertical pali, columellae, and mural trabeculae predominate in both transverse and longitudinal thin-sections.

Figure

1. Figured Specimen. NMB D5811.
   Lower Pliocene, NMB locality 16826, Río Cana, Gurabo Formation, Dominican Republic. Colony fragments as preserved within the sediment matrix, ×1.
2. Figured Specimen. NMB D5812.
   Upper Miocene, NMB locality 16883, Río Gurabo, Gurabo Formation, Dominican Republic. Branch surface, ×1.
3. Figured Specimen. USNM 325105a.
   Middle Miocene, USGS locality 6106, La Boca Formation, Panama. Branch surface, ×1 (holotype of *Porites toulai* Vaughan).
4. Holotype. USNM 325069.
   Upper Pliocene, USGS locality 3476, Baracoa, Cuba. Branch surface, ×1.
5. Figured Specimen. USNM 325067a.
   Upper Pliocene, USGS locality 3461, Matanzas, Cuba. Branch surface, ×1 (holotype of *Porites baracoaensis matanzasensis* Vaughan).
6. Possible synonym, lectotype of *Porites douvillei* Vaughan. USNM 325106.
   Middle Miocene, USGS locality 6016, La Boca Formation, Panama. Branch surface, ×1.
7. Figured Specimen. NMB D5813.
   Upper Miocene, NMB locality 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Branch surface, ×1.
8. Figured Specimen. NMB D5814.
   Upper Miocene, NMB locality 16811, Río Gurabo, Gurabo Formation, Dominican Republic. Branch surface, ×1.
9. Figured Specimen. NMB D5815.
   Upper Miocene, NMB locality 15859, Río Gurabo, Gurabo Formation, Dominican Republic. Branch surface, ×1.
10. Figured Specimen. NMB D5816.
    Upper Miocene, NMB locality 15849, Río Gurabo, Gurabo Formation, Dominican Republic. Thin-section cut perpendicular to branch axis, ×5.
11. Figured Specimen. NMB D5817.
    Upper Miocene, NMB locality 16811, Río Gurabo, Gurabo Formation, Dominican Republic. Thin-section cut perpendicular to branch axis, ×5.
12. Figured Specimen. NMB D5817.
    Same specimen as figure 11 above. Transverse thin-section, ×25, showing one complete corallite (upper left) and portions of three others.
13. Figured Specimen. NMB D5818.
    Upper Miocene, NMB locality 16934, Río Gurabo, Gurabo Formation, Dominican Republic. Longitudinal thin-section, ×25, through one complete corallite.

EXPLANATION OF PLATE 17

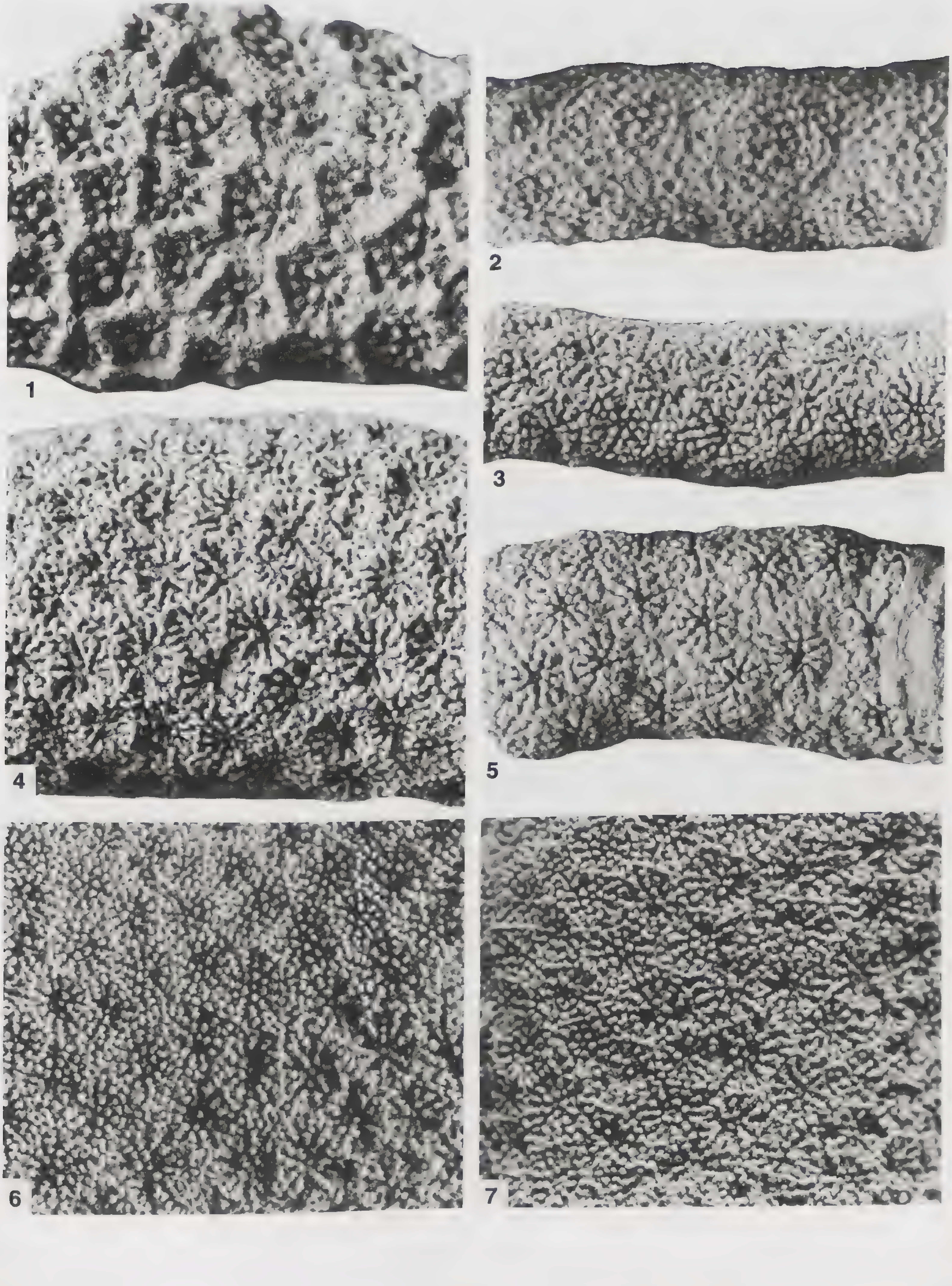
Page

Porites baracoaensis Vaughan 75

Close-ups of calical surfaces. Calyx characters vary considerably. A thin, denser wall, low calice elevation, prominent pali, and a small corallite diameter are characteristic.

Figure

1. Holotype. USNM 325069.
   Same specimen as Plate 16, figure 4. Calical surface, ×10.
2. Figured Specimen. USNM 325067a.
   Same specimen as Plate 16, figure 5. Calical surface, ×10.
3. Figured Specimen. NMB D5812.
   Same specimen as Plate 16, figure 2. Calical surface, ×10.
4. Figured Specimen. NMB D5819.
   Upper Miocene, NMB locality 15849, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
5. Figured Specimen. NMB D5820.
   Upper Miocene, NMB locality 15856, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
6. Figured Specimen. NMB D5815.
   Same specimen as Plate 16, figure 9. Calical surface, ×10.
7. Figured Specimen. NMB D5813.
   Same specimen as Plate 16, figure 7. Calical surface, ×10.



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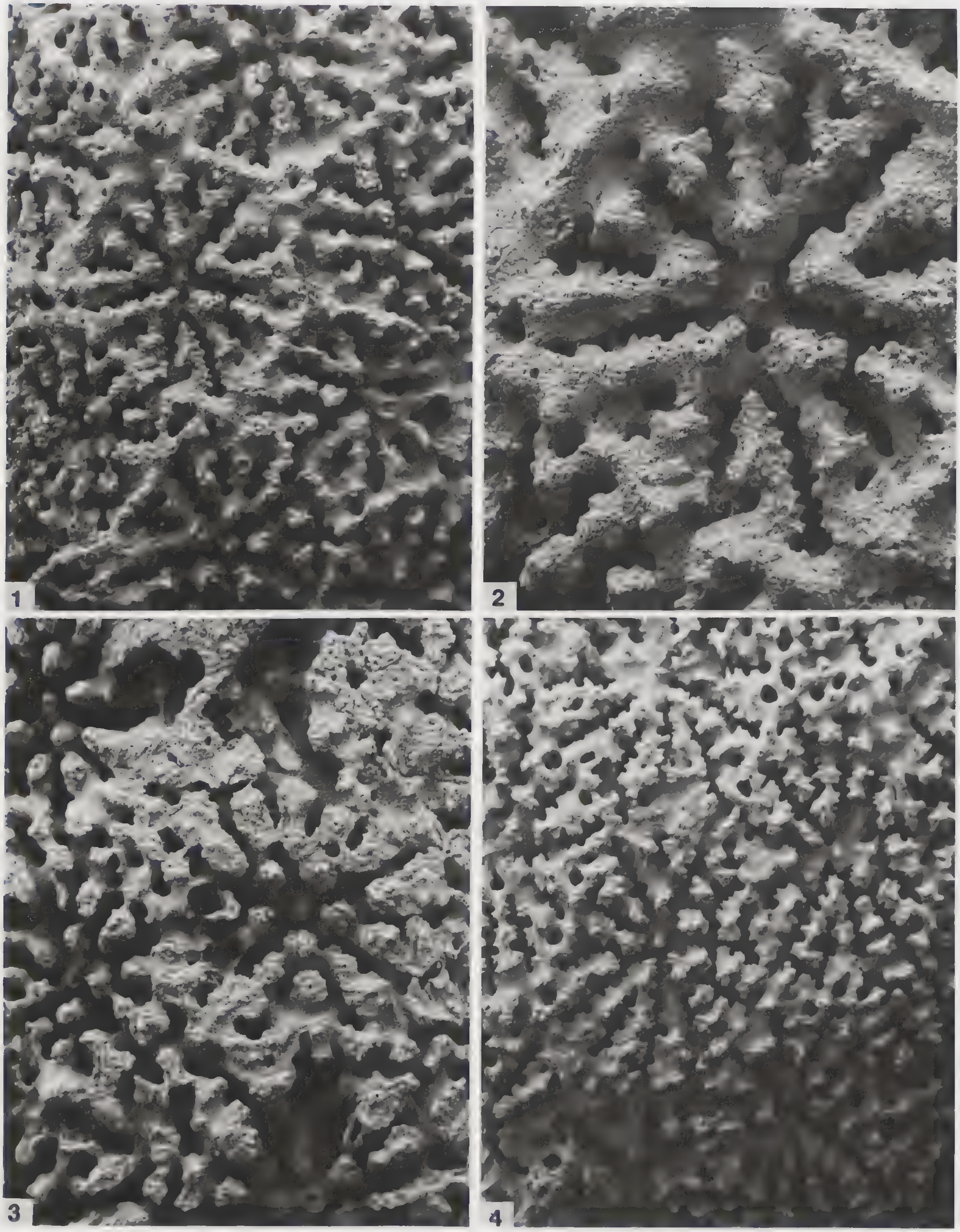
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EXPLANATION OF PLATE 18

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Porites baracoaensis Vaughan 75

SEM photographs of calices. Of all the Neogene Dominican Republic *Porites,* this species has the most well-developed pali and columella tubercle. The wall commonly consists of a single prominent trabecular row as seen in figures 1 and 2.

Figure

1. Figured Specimen. NMB D5821.
   Upper Miocene, NMB locality 16811, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.
2. Figured Specimen. NMB D5821.
   Same specimen as figure 1 above, ×67.
3. Figured Specimen. NMB D5822.
   Upper Miocene, NMB locality 16811, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.
4. Figured Specimen. NMB D5823.
   Upper Miocene, NMB locality 15853, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.

EXPLANATION OF PLATE 19

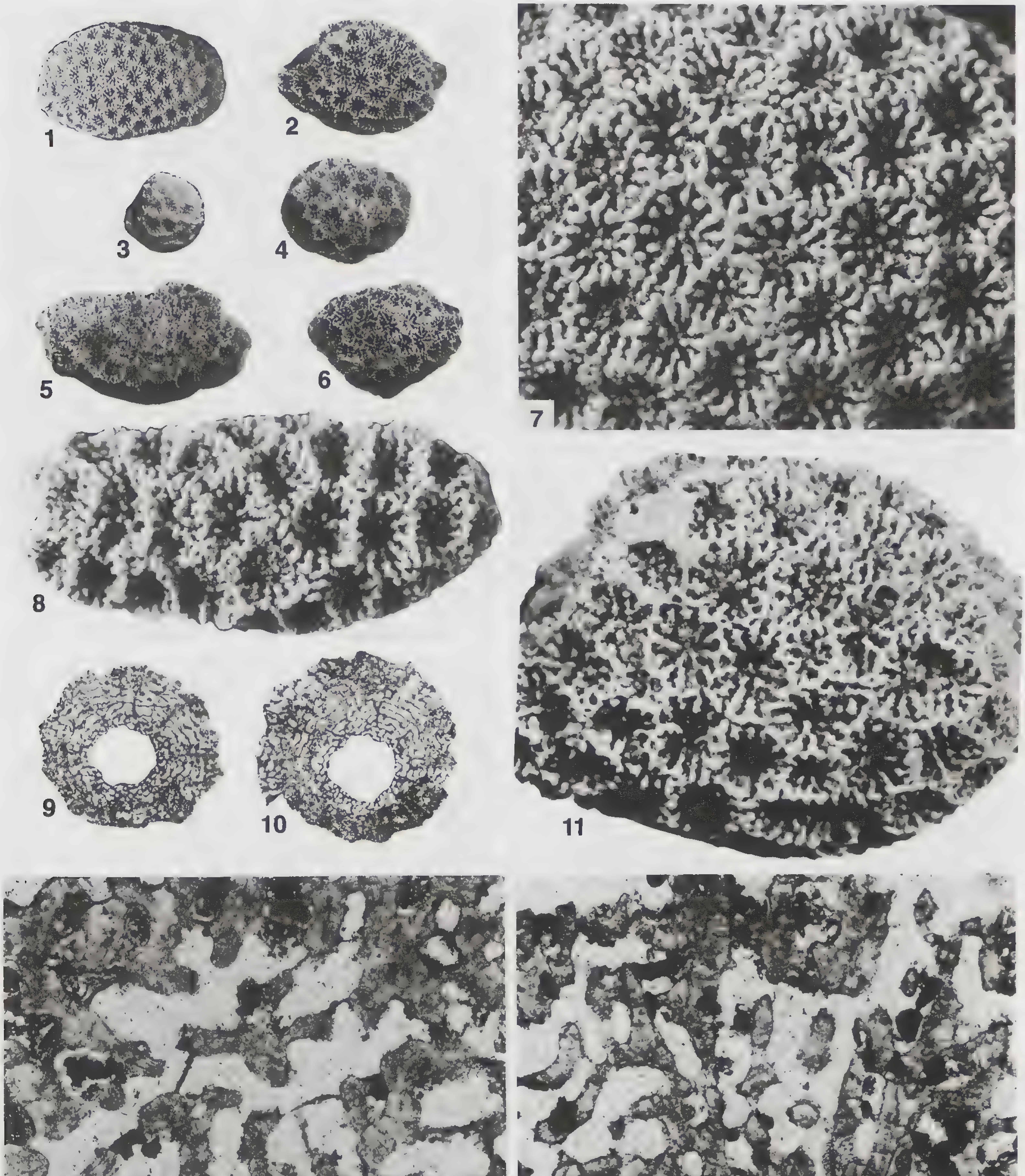
Page

Porites convivatoris, new species 76

Colony surfaces and thin-sections. Colonies consist of small ellipsoids. A calcareous tube always extends down the long axis. Calices are highly elevated and separated by a single prominent row of mural trabeculae. In thin-section, vertical trabeculae and dissepiments dominate the morphology. Horizontal septal junctions are rare.

Figure

1. Holotype. NMB D5830.
   Upper Miocene, NMB locality 16852, Río Cana, Cercado Formation, Dominican Republic. Whole colony, ×2.
2. Paratype. NMB D5833.
   Upper Miocene, NMB locality 16836, Río Cana, Cercado Formation, Dominican Republic. Whole colony, ×2.
3. Paratype. NMB D5832.
   Lower Pliocene, NMB locality 16879, Río Cana, Gurabo Formation, Dominican Republic. Whole colony, ×2.
4. Figured Specimen. USNM 64669.
   Upper Miocene, USGS locality 8525, Río Mao, ?Cercado Formation, Dominican Republic. Whole colony, ×2.
5. Figured Specimen. USNM 64669.
   Same locality as figure 4 above. Whole colony, ×2.
6. Paratype. NMB D5834.
   Upper Miocene, NMB locality 16836, Río Cana, Cercado Formation, Dominican Republic. Whole colony, ×2.
7. Holotype. NMB D5830.
   Same specimen as figure 1 above. Calical surface, ×10.
8. Paratype. NMB D5831.
   Upper Miocene, NMB locality 16928, Río Mao, Cercado Formation, Dominican Republic. Whole colony, ×10.
9. Paratype. NMB D5835.
   Upper Miocene, NMB locality 16922, Río Mao, Cercado Formation, Dominican Republic. Thin-section cut perpendicular to the tube, ×5.
10. Paratype. NMB D5836.
    Upper Miocene, NMB locality 16928, Río Mao, Cercado Formation, Dominican Republic. Thin-section cut perpendicular to the tube, ×5.
11. Paratype. NMB D5833.
    Same specimen as figure 2 above. Calical surface, ×10.
12. Paratype. NMB D5837.
    Upper Miocene, NMB locality 16928, Río Mao, Cercado Formation, Dominican Republic. Transverse thin-section, ×25, showing one complete corallite.
13. Paratype. NMB D5838.
    Upper Miocene, NMB locality 16839, Río Cana, Cercado Formation, Dominican Republic. Longitudinal thin-section, ×25, showing the wall between two corallites.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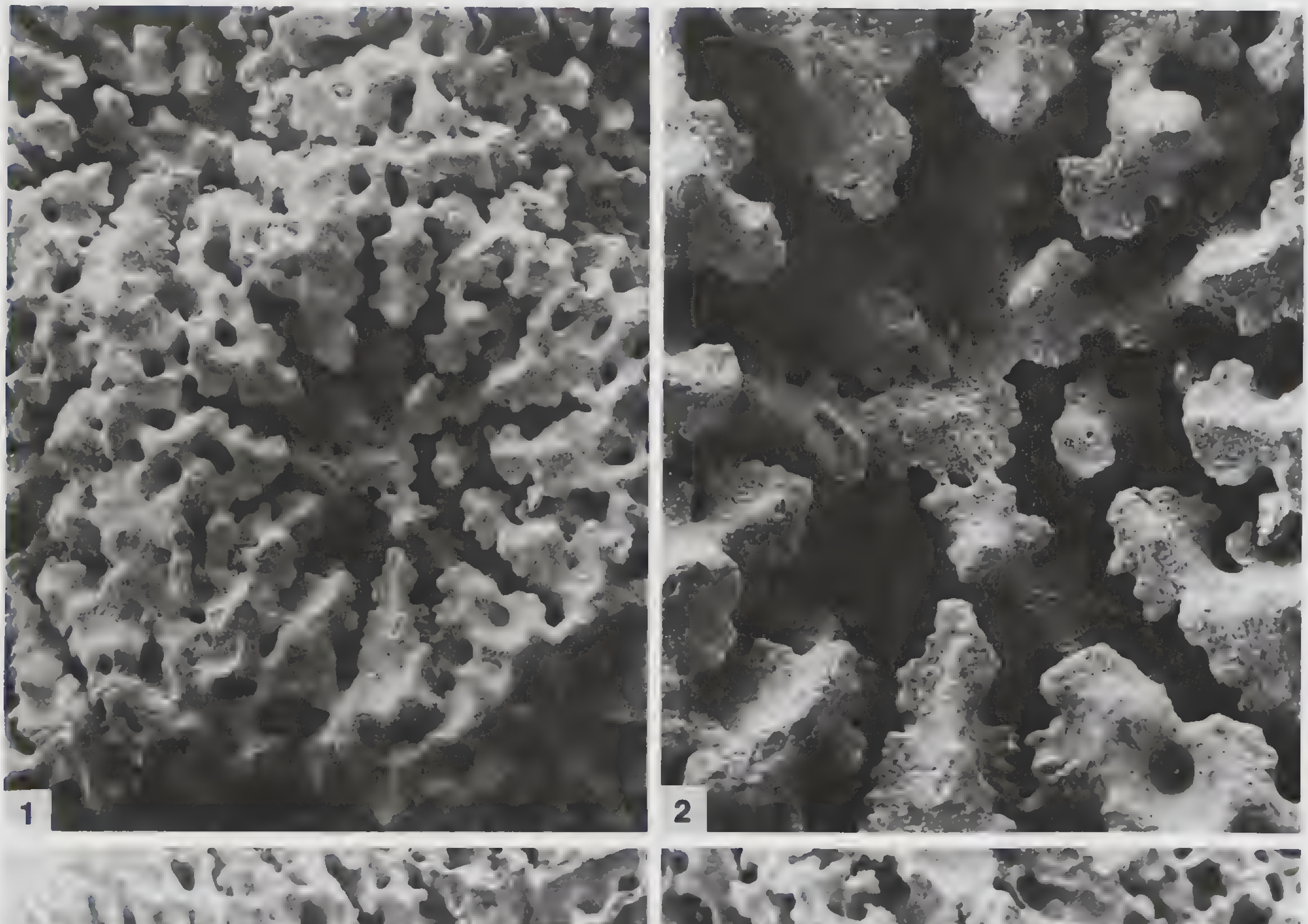
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EXPLANATION OF PLATE 20

Page

Porites convivatoris, new species 76

SEM photographs of calices. Calices are elevated and have approximately five thin pali and a thin columella tubercle. Septa are usually heavily ornamented.

Figure

1. Paratype. NMB D5839.
   Upper Miocene, NMB locality 16928, Río Mao, Cercado Formation, Dominican Republic, ×28.
2. Paratype. NMB D5839.
   Same specimen as figure 1 above, ×67.
3. Paratype. NMB D5840.
   Upper Miocene, NMB locality 16836, Río Cana, Cercado Formation, Dominican Republic, ×28.
4. Paratype. NMB D5841.
   Upper Miocene, NMB locality 16928, Río Mao, Cercado Formation, Dominican Republic, ×28.

EXPLANATION OF PLATE 21

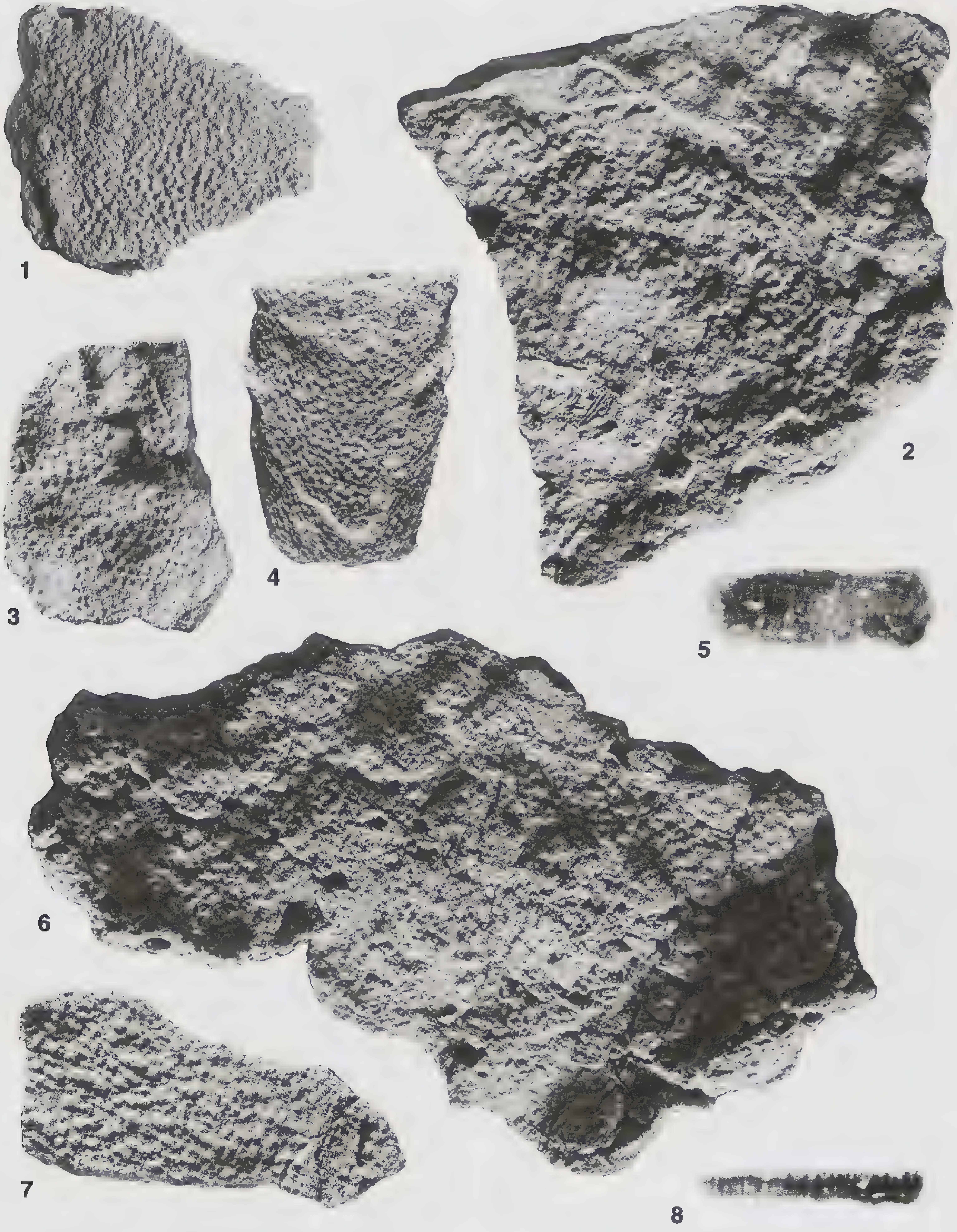
Page

Porites macdonaldi Vaughan 78

Colony fragments and X-radiographs of colonies. The colony morphology consists primarily of plates with growth bands at 1 to 2 mm intervals. Ridges of coenosteal reticulum commonly extend irregularly across the plate surface. Valleys between ridges are formed by series of calices produced by intratentacular budding. X-radiographs show that horizontal septal junctions dominate the internal structure.

Figure

1. Lectotype. USNM 72376.
   Middle Miocene, USGS locality 6016, La Boca Formation, Panama. Fragment of a plate-shaped colony, ×1.
2. Figured Specimen. NMB D5842.
   Upper Miocene, NMB locality 16921, Río Gurabo, Gurabo Formation, Dominican Republic. Plate-shaped colony, ×1.
3. Figured Specimen. NMB D5843.
   Upper Miocene, NMB locality 15841, Río Gurabo, Gurabo Formation, Dominican Republic. Plate-shaped colony fragment, ×1.
4. Paralectotype. USNM 325046a.
   Middle Miocene, USGS locality 6016, La Boca Formation, Panama. Colony fragment, ×1.
5. Figured Specimen. NMB D5844.
   Upper Miocene, NMB locality 16933, Río Gurabo, Gurabo Formation, Dominican Republic. X-radiograph, ×1.
6. Figured Specimen. NMB D5845.
   Upper Miocene, NMB locality 16911, Río Mao, ?Gurabo Formation, Dominican Republic. Plate-shaped colony, ×1.
7. Figured Specimen. NMB D5846.
   Upper Miocene, NMB locality 16883, Río Gurabo, Gurabo Formation, Dominican Republic. Plate-shaped colony fragment, ×1.
8. Figured Specimen. NMB D5847.
   Lower Pliocene, NMB locality 15826, Río Gurabo, Mao Formation, Dominican Republic. X-radiograph, ×1.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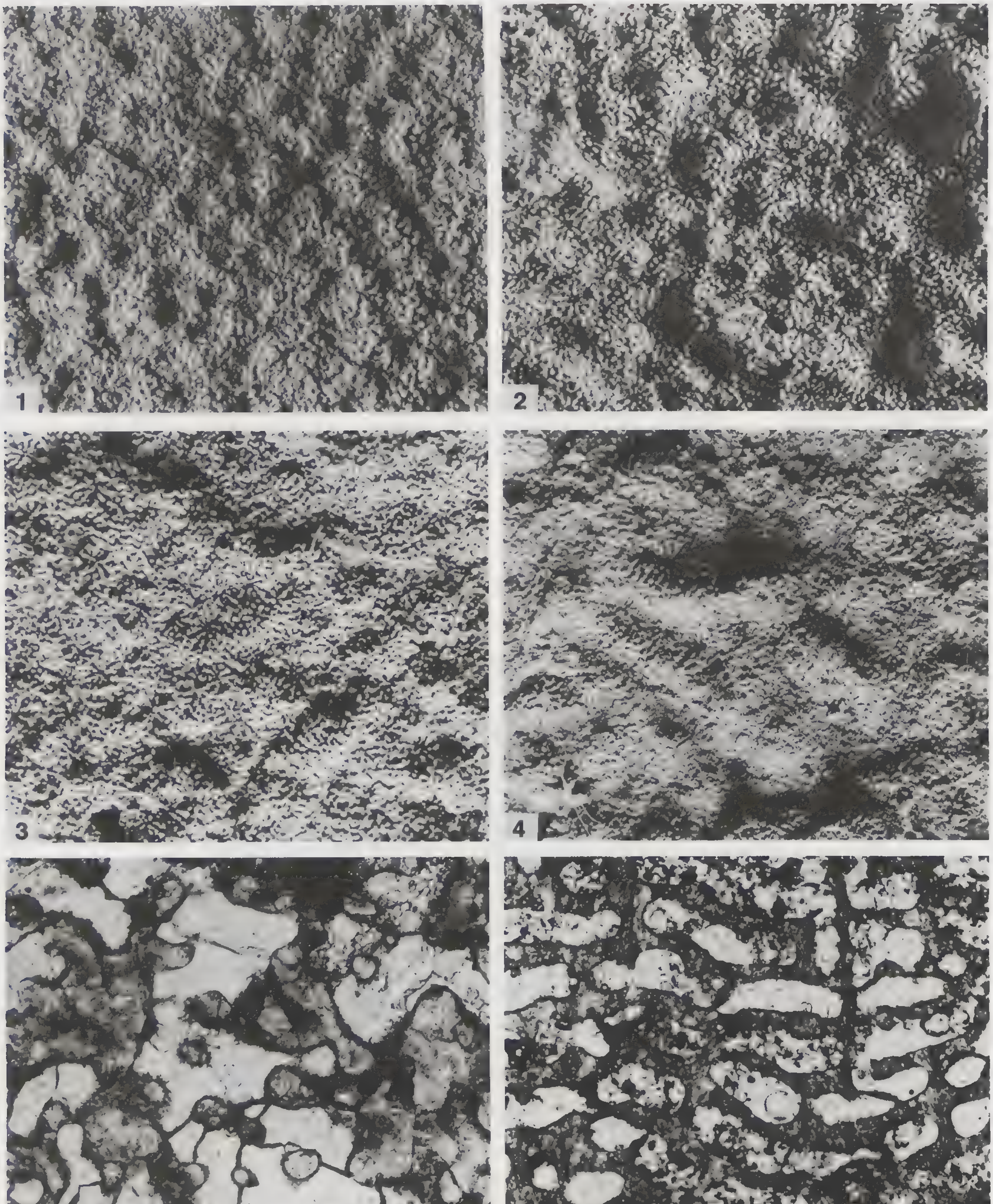
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EXPLANATION OF PLATE 22

Page

Porites macdonaldi Vaughan 78

Close-ups of calical surfaces and thin-sections. The calical surface is composed of extensive coenosteal reticulum that may form irregular ridges between corallite rows. The calices themselves appear small and superficial. Thin-sections show well-developed horizontal septal junctions, weakly-developed vertical trabeculae, and prominent granulations.

Figure

1. Lectotype. USNM 72376.
   Same specimen as Plate 21, figure 1. Calical surface, ×5.
2. Figured Specimen. NMB D5846.
   Same specimen as Plate 21, figure 7. Calical surface, ×5.
3. Figured Specimen. NMB D5845.
   Same specimen as Plate 21, figure 6. Calical surface, ×5.
4. Figured Specimen. NMB D5842.
   Same specimen as Plate 21, figure 2. Calical surface, ×5.
5. Figured Specimen. NMB D5848.
   Upper Miocene, NMB locality 16911. Río Mao, ?Gurabo Formation, Dominican Republic. Transverse thin-section, ×25, showing one complete corallite.
6. Figured Specimen. NMB D5849.
   Upper Miocene, NMB locality 15846, Río Gurabo, Gurabo Formation, Dominican Republic. Longitudinal thin-section, ×25, showing the wall between two corallites.

EXPLANATION OF PLATE 23

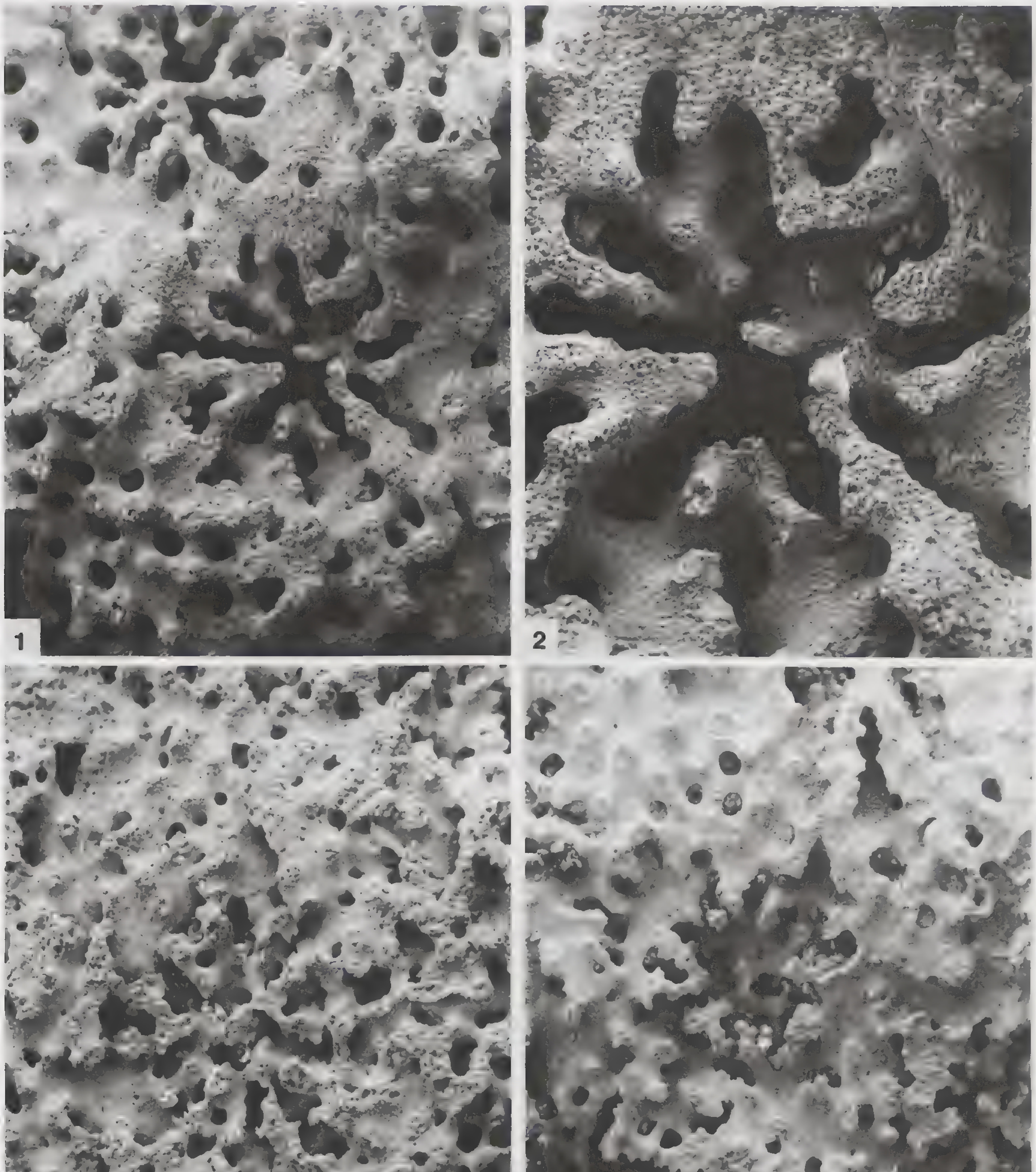
Page

Porites macdonaldi Vaughan 78

SEM photographs of calices. Calices are fairly shallow with poorly developed pali and a prominent columella tubercle. The columellar synapticular ring is wide, and the septa do not always extend completely to it.

Figure

1. Figured Specimen. NMB D5847.
   Same specimen as Plate 21, figure 8, ×28.
2. Figured Specimen. NMB D5847.
   Same specimen as figure 1 above, ×67.
3. Figured Specimen. NMB D5850.
   Lower Pliocene, NMB locality 15824, Río Gurabo, Mao Formation, Dominican Republic, ×28.
4. Figured Specimen. NMB D5851.
   Upper Miocene, NMB locality 16883, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.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EXPLANATION OF PLATE 24

Page

Porites portoricensis (Vaughan) 79

Branch fragments and thin-sections cut perpendicular to branch axes. The colony morphology is highly variable, ranging from thin branches to columns with skirts. Only one relatively complete colony has been found. Thin-sections cut perpendicular to each branch axis show a porous reticulum at the core of the axis, which is surrounded by uniform, prominent, widely-spaced horizontal septal junctions that may be crossed by vertical trabeculae.

Figure

1. Holotype. USNM 325061.
   Lower Miocene, USGS locality 3191, Lares Formation, Puerto Rico. Branch surface, ×1.
2. Figured Specimen. PIU WI9.
   Lower Miocene, Anguilla Formation, Anguilla. Branch surface, ×1 (paratype of *Goniopora clevei* Vaughan).
3. Figured Specimen. USNM 325115.
   Lower Miocene, USGS locality 6966, Anguilla Formation, Anguilla. Branch surface, ×1 (paratype of *Goniopora clevei* Vaughan).
4. Figured Specimen. USNM 325072.
   Middle Miocene, USGS locality 6020, La Boca Formation, Panama. Branch surface, ×1 (holotype of *Goniopora cascadensis* Vaughan).
5. Figured Specimen. USNM 68315.
   Lower Miocene, USGS locality 6546, Tampa Formation, Florida. Branch surface, ×1 (holotype of *Goniopora matsoni* Weisbord).
6. Possible synonym, lectotype of *Porites* (*Synaraea*) *howei* Vaughan. USNM 72890.
   Middle Miocene, USGS locality 6016, La Boca Formation, Panama. Branch surface, ×1.
7. Figured Specimen. NMB D5796.
   Upper Miocene, NMB locality 15851, Río Gurabo, Gurabo Formation, Dominican Republic. Branch surface, ×1.
8. Figured Specimen. BM(NH) R28828.
   Neogene, Nivajé Shale, Dominican Republic. Branch surface, ×1 (Duncan's specimen of *Alveopora fenestra* Dana).
9. Figured Specimen. NMB D5797.
   Upper Miocene, NMB locality 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Branch surface, ×1.
10. Figured Specimen. NMB D5798.
    Lower Pliocene, NMB locality 15821, Río Gurabo, Mao Formation, Dominican Republic. Branch surface, ×1.
11. Figured Specimen. NMB D5799.
    Upper Miocene, NMB locality 16883, Río Gurabo, Gurabo Formation, Dominican Republic. Branch surface, ×1.
12. Figured Specimen. NMB D5800.
    Lower Pliocene, NMB locality 16884, Río Cana, Mao Formation, Dominican Republic. Branch surface, ×1.
13. Figured Specimen. NMB D5802.
    Upper Miocene, NMB locality 15853, Río Gurabo, Gurabo Formation, Dominican Republic. Thin-section, ×5.
14. Figured Specimen. NMB D5803.
    Upper Miocene, NMB locality 15855, Río Gurabo, Gurabo Formation, Dominican Republic. Thin-section, ×5.
15. Figured Specimen. NMB D5801.
    Upper Miocene, NMB locality 16933, Río Gurabo, Gurabo Formation, Dominican Republic. Thin-section, ×5.

EXPLANATION OF PLATE 25

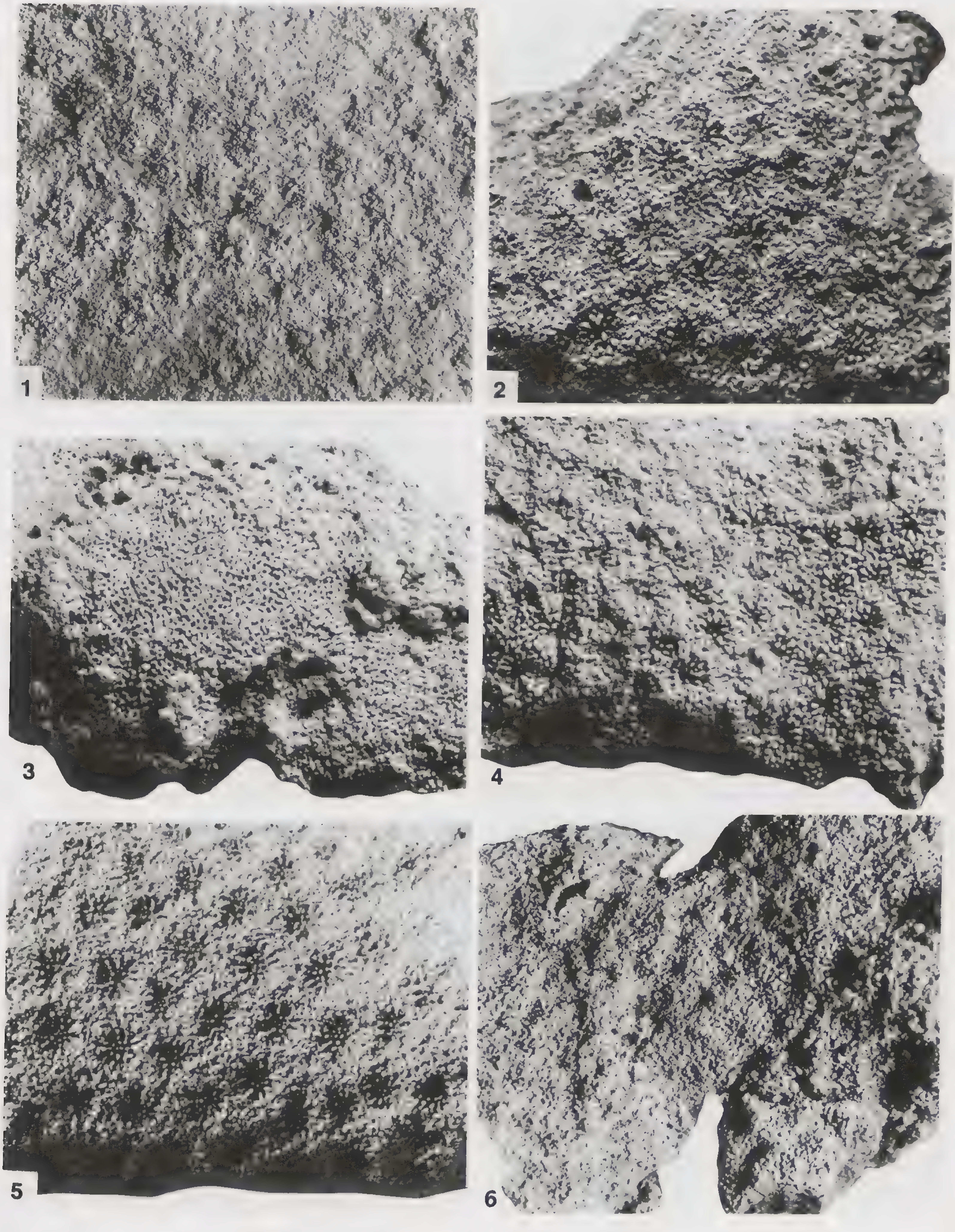
Page

Porites portoricensis (Vaughan) 79

Close-ups of calical surfaces. Calices vary widely in many characters; however, they are generally large and separated by an extensive coenosteal reticulum. Septal denticles are frequently well-developed.

Figure

1. Holotype. USNM 325061.
   Same specimen as Plate 24, figure 1. Calical surface, ×5.
2. Figured Specimen. USNM 25072.
   Same specimen as Plate 24, figure 4. Calical surface, ×5.
3. Figured Specimen. PIU WI10.
   Lower Miocene, Anguilla Formation, Anguilla. Calical surface, ×5 (holotype of *Goniopora clevei* Vaughan).
4. Figured Specimen. PIU WI9.
   Same specimen as Plate 24, figure 2. Calical surface, ×5.
5. Figured Specimen. USNM 68315.
   Same specimen as Plate 24, figure 5. Calical surface, ×5.
6. Figured Specimen. USNM 325113.
   Same specimen as Plate 24, figure 6. Calical surface, ×5.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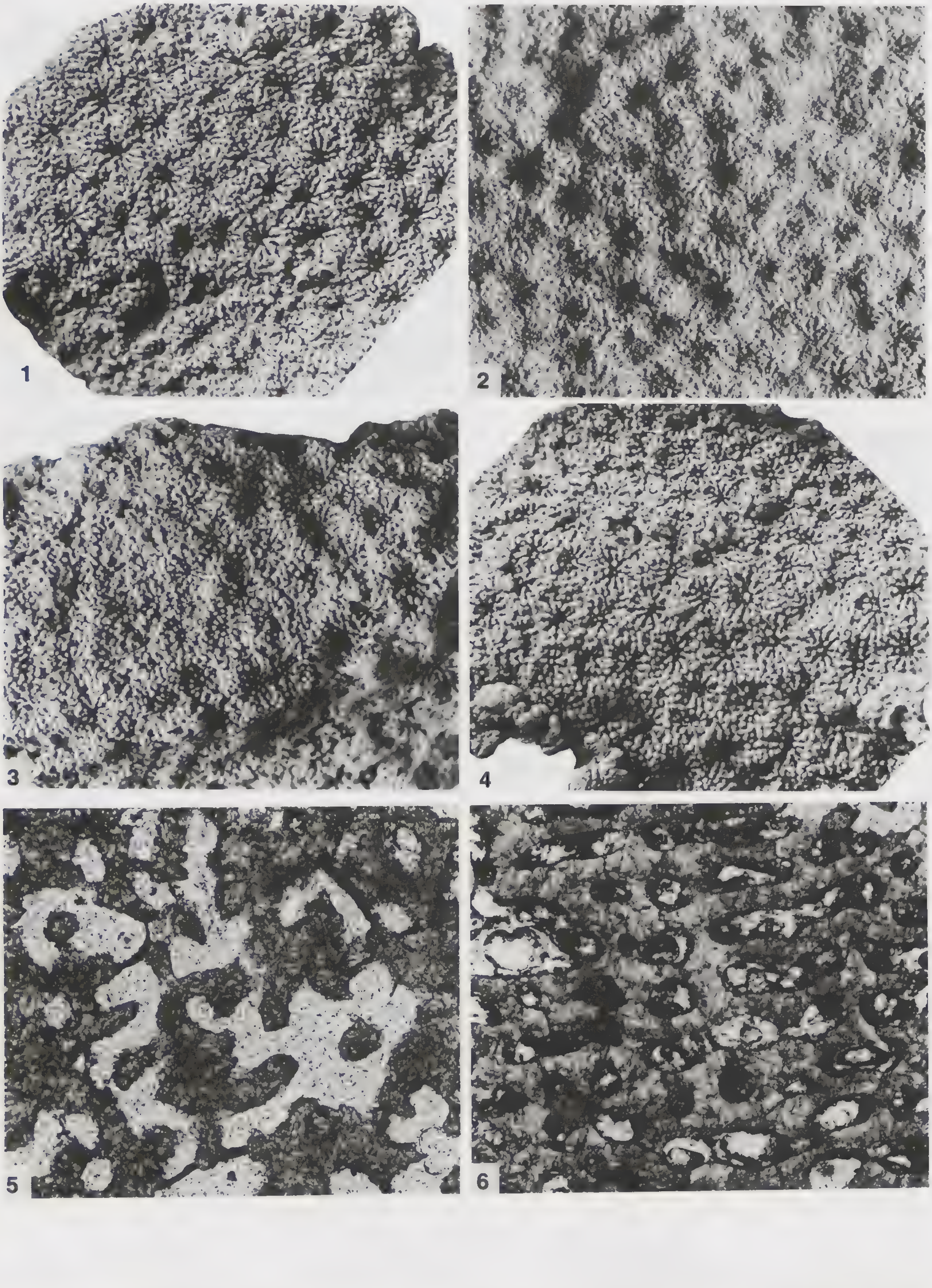
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6

EXPLANATION OF PLATE 26

Page

Porites portoricensis (Vaughan) 79

Close-ups of calical surfaces and thin-sections. As in Plate 25, calices appear variable in many characteristics but are generally large and separated by a well-developed coenosteal reticulum. Thin-sections show the irregular development of vertical trabeculae, the prominent denticles, and the most common wall structure, which consists of three mural trabecular rows.

Figure

1. Figured Specimen. NMB D5797.
   Same specimen as Plate 24, figure 9. Calical surface, ×5.
2. Figured Specimen. NMB D5800.
   Same specimen as Plate 24, figure 12. Calical surface, ×5.
3. Figured Specimen. NMB D5796.
   Same specimen as Plate 24, figure 7. Calical surface, ×5.
4. Figured Specimen. NMB D5798.
   Same specimen as Plate 24, figure 10. Calical surface, ×5.
5. Figured Specimen. NMB D5801.
   Same specimen as Plate 24, figure 15. Transverse thin-section, ×25, showing one corallite.
6. Figured Specimen. NMB D5804.
   Upper Miocene, NMB locality 16883, Río Gurabo, Gurabo Formation, Dominican Republic. Longitudinal thin-section, ×25, showing mural trabeculae between two corallites.

EXPLANATION OF PLATE 27

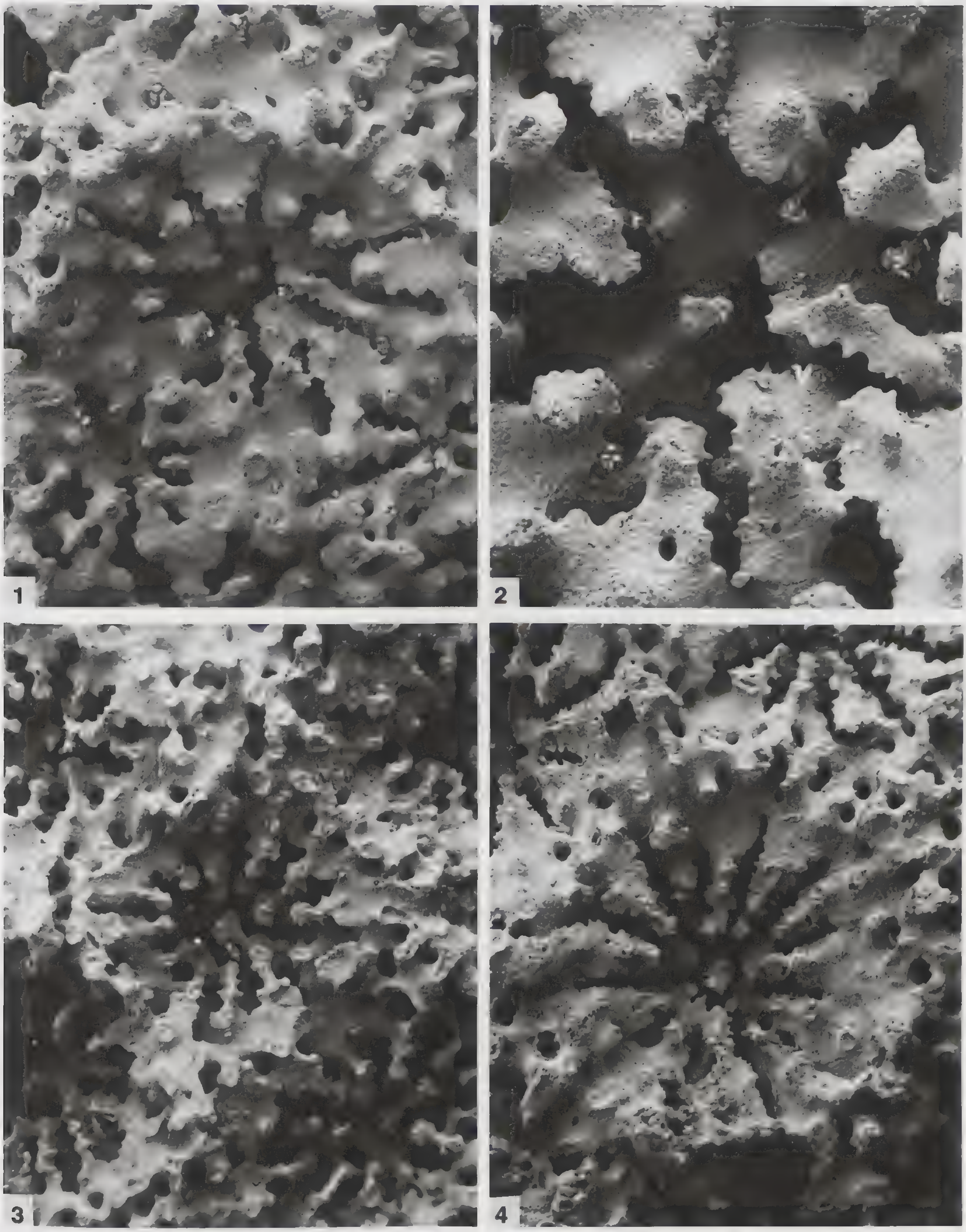
Page

Porites portoricensis (Vaughan) 79

SEM photographs of calices. Septa commonly bifurcate to give a *Goniopora*-like appearance. They are frequently formed by horizontal flakes with prominent denticles. Pali are weakly-developed; however, a small columella tubercle is usually present.

Figure

1. Figured Specimen. NMB D5805.
   Upper Miocene, NMB locality 16811, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.
2. Figured Specimen. NMB D5805.
   Same specimen as in figure 1 above, ×67.
3. Figured Specimen. NMB D5806.
   Upper Miocene, NMB locality 16934, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.
4. Figured Specimen. NMB D5807.
   Upper Miocene, NMB locality 16883, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.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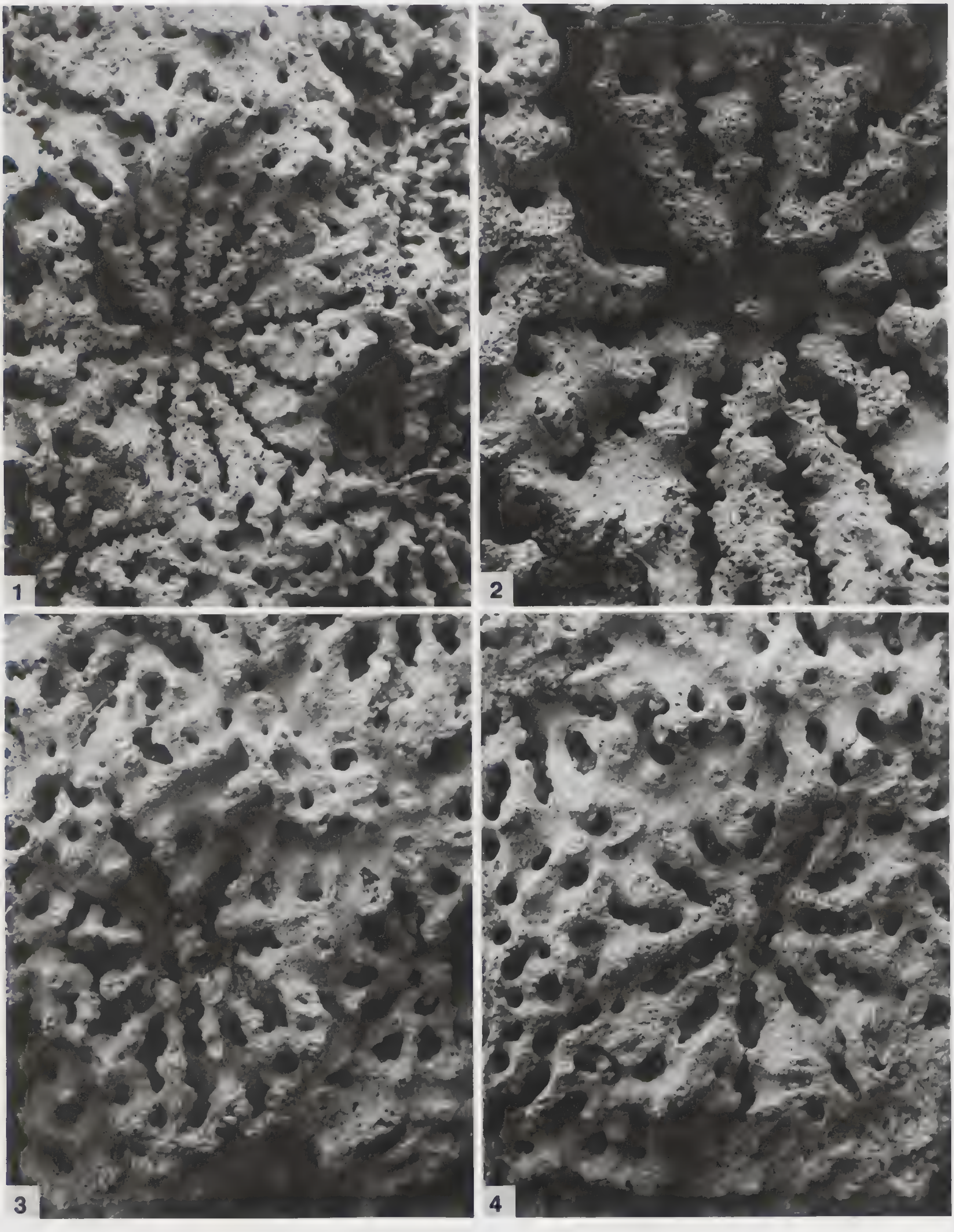
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EXPLANATION OF PLATE 28

Page

Porites portoricensis (Vaughan) 79

SEM photographs of calices. In more worn material, the flaky texture of the septa is less apparent and the coenosteal reticulum dominates the surface morphology.

Figure

1. Figured Specimen. NMB D5808.
   Upper Miocene, NMB locality 15851, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.
2. Figured Specimen. NMB D5808.
   Same specimen as figure 1 above, ×67.
3. Figured Specimen. NMB D5809.
   Lower Pliocene, NMB locality 15821, Río Gurabo, Mao Formation, Dominican Republic, ×28.
4. Figured Specimen. NMB D5810.
   Lower Pliocene, NMB locality 16884, Río Cana, Mao Formation, Dominican Republic, ×28.

EXPLANATION OF PLATE 29

Page

Porites waylandi, nom. nov. 81

Whole colonies. Colony morphology is massive, ranging in shape from columns to hemispherical mounds to plates.

Figure

1. Holotype. USNM 325063.
   Middle Miocene, USGS locality 6016, La Boca Formation, Panama. Upper surface of a plate, ×1.
2. Figured Specimen. USNM 66220.
   Lower Miocene, Ballast Point, Tampa Formation, Florida. Side of a nodular column, ×1 (one of Wesibord's nontype specimens of "*Porites floridaprima* Bernard").
3. Figured Specimen. NMB D5824.
   Upper Miocene, NMB locality 16811, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of a plate, ×½.
4. Figured Specimen. NMB D5825.
   Upper Miocene, NMB locality 16933, Río Gurabo, Gurabo Formation, Dominican Republic. Side of a smooth column, ×1.

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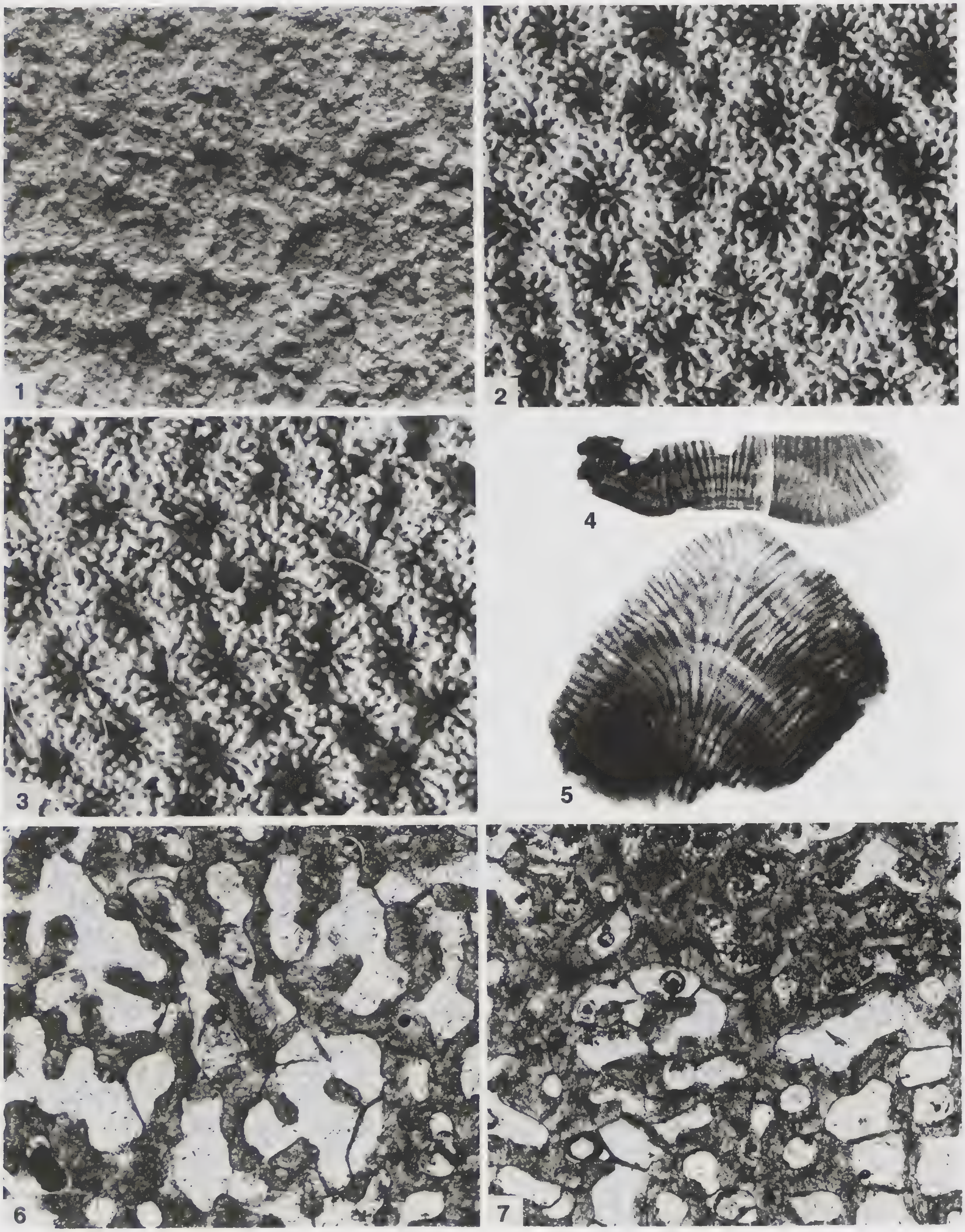


EXPLANATION OF PLATE 30

Page
Porites waylandi, nom. nov. 81

Close-ups of calical surfaces, thin-sections, and X-radiographs of colonies. This species is distinguished by a thick, porous wall, poorly-developed pali, a small columella tubercle, and septa that extend completely to the columella synapticular ring. X-radiographs and thin-sections show that growth was approximately 2 to 3 mm per year and that synapticulae, dissepiments, and trabeculae around the columella are especially well-developed.

Figure

1. Holotype. USNM 325063.
   Same specimen as Plate 29, figure 1. Calical surface, ×10.
2. Figured Specimen. USNM 66220.
   Same specimen as Plate 29, figure 2. Calical surface, ×10.
3. Figured Specimen. NMB D5825.
   Same specimen as Plate 29, figure 4. Calical surface, ×10.
4. Figured Specimen. NMB D5827.
   Lower Miocene, NMB locality 17284, Río Yaque del Norte, Baitoa Formation, Dominican Republic. X-radiograph, ×1.
5. Figured Specimen. NMB D5826.
   Upper Miocene, NMB locality 16856, Río Cana, Cercado Formation, Dominican Republic. X-radiograph, ×1.
6. Figured Specimen. NMB D5826.
   Same specimen as figure 5. Transverse thin-section, ×25, showing one complete corallite.
7. Figured Specimen. NMB D5826.
   Same specimen as figure 5. Longitudinal thin-section, ×25, showing one complete corallite.

EXPLANATION OF PLATE 31

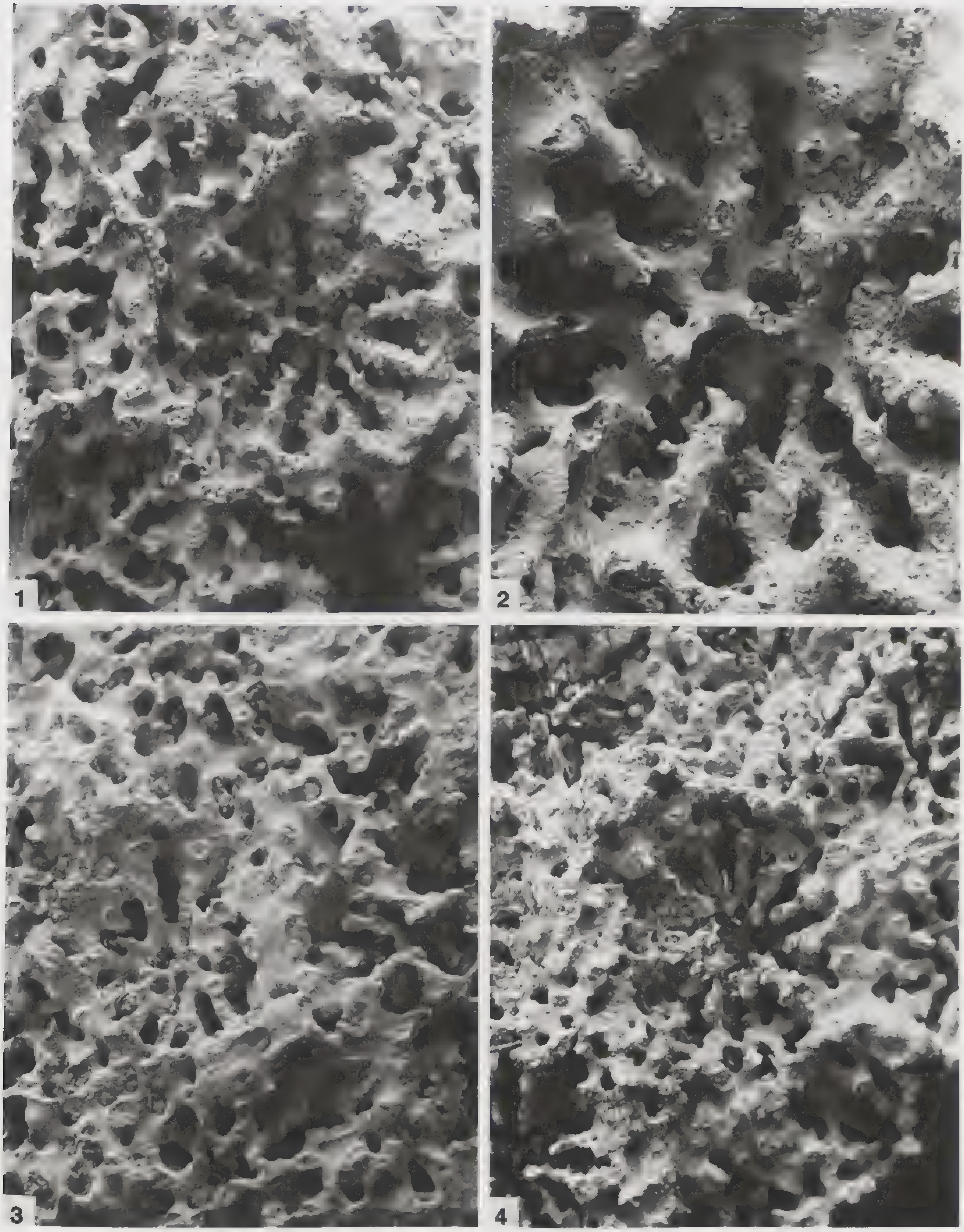
Page

Porites waylandi, nom. nov. 81

SEM photographs of calices. Septa extend completely to the columellar synapticular ring, which connects a well-developed network of trabeculae. The pali and columella tubercle are poorly-developed or absent.

Figure

1. Figured Specimen. NMB D5828.
   Upper Miocene, NMB locality 15846, Río Gurabo, Gurabo Formation, Dominican Republic, ×28.
2. Figured Specimen. NMB D5828.
   Same specimen as figure 1 above, ×67.
3. Figured Specimen. NMB D5826.
   Same specimen as Plate 30, figures 4, 5, and 7, ×28.
4. Figured Specimen. NMB D5829.
   Lower Miocene, NMB locality 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic, ×28.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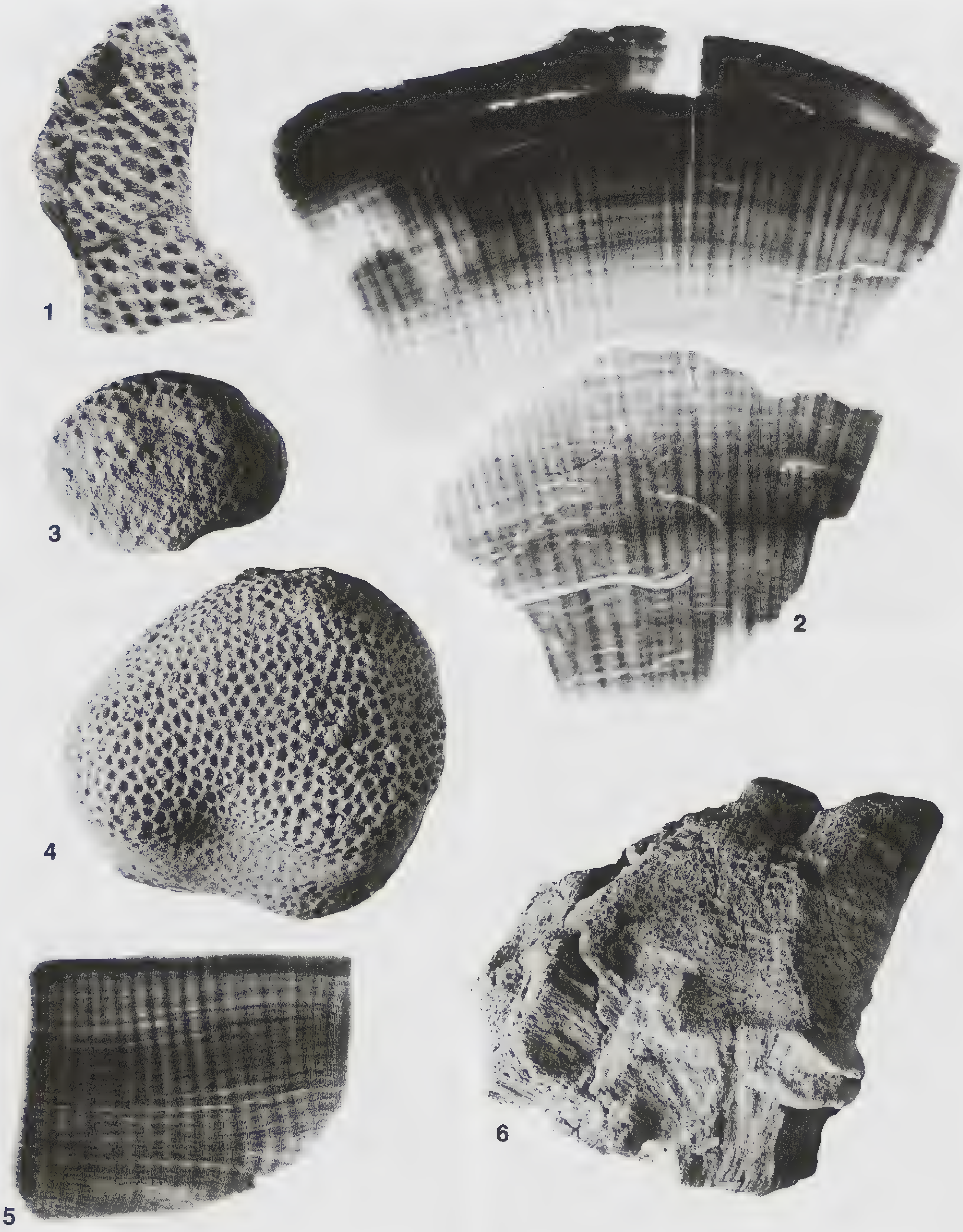
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EXPLANATION OF PLATE 32

Page
Goniopora hilli Vaughan 83

Whole colonies and X-radiographs of colonies. Colonies generally have smooth, hemispherical mound shapes that may be as large as 30 to 50 cm in diameter. Growth bands occur regularly at intervals of 3 to 4 mm.

Figure
1. Holotype. USNM 325058.
   Middle Miocene, USGS locality 6016. La Boca Formation, Panama. Upper surface of colony fragment, ×1.
2. Figured Specimen. NMB D5852.
   Lower Miocene, NMB locality 16937, Río Yaque del Norte, Baitoa Formation, Dominican Republic. X-radiograph, ×1.
3. Figured Specimen. USNM 68317.
   Lower Miocene, USGS locality 2084, Tampa Formation, Florida. Side view of colony, ×1 (holotype of *Goniopora tampaensis* Weisbord).
4. Figured Specimen. NMB D5853.
   Upper Miocene, NMB locality 15861, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of colony, ×1.
5. Figured Specimen. NMB D5854.
   Upper Miocene, NMB locality 16933, Río Gurabo, Gurabo Formation, Dominican Republic. X-radiograph, ×1.
6. Figured Specimen. NMB D5855.
   Lower Pliocene, NMB locality 16818, Río Cana, Gurabo Formation, Dominican Republic. Side view of large colony, ×¼.

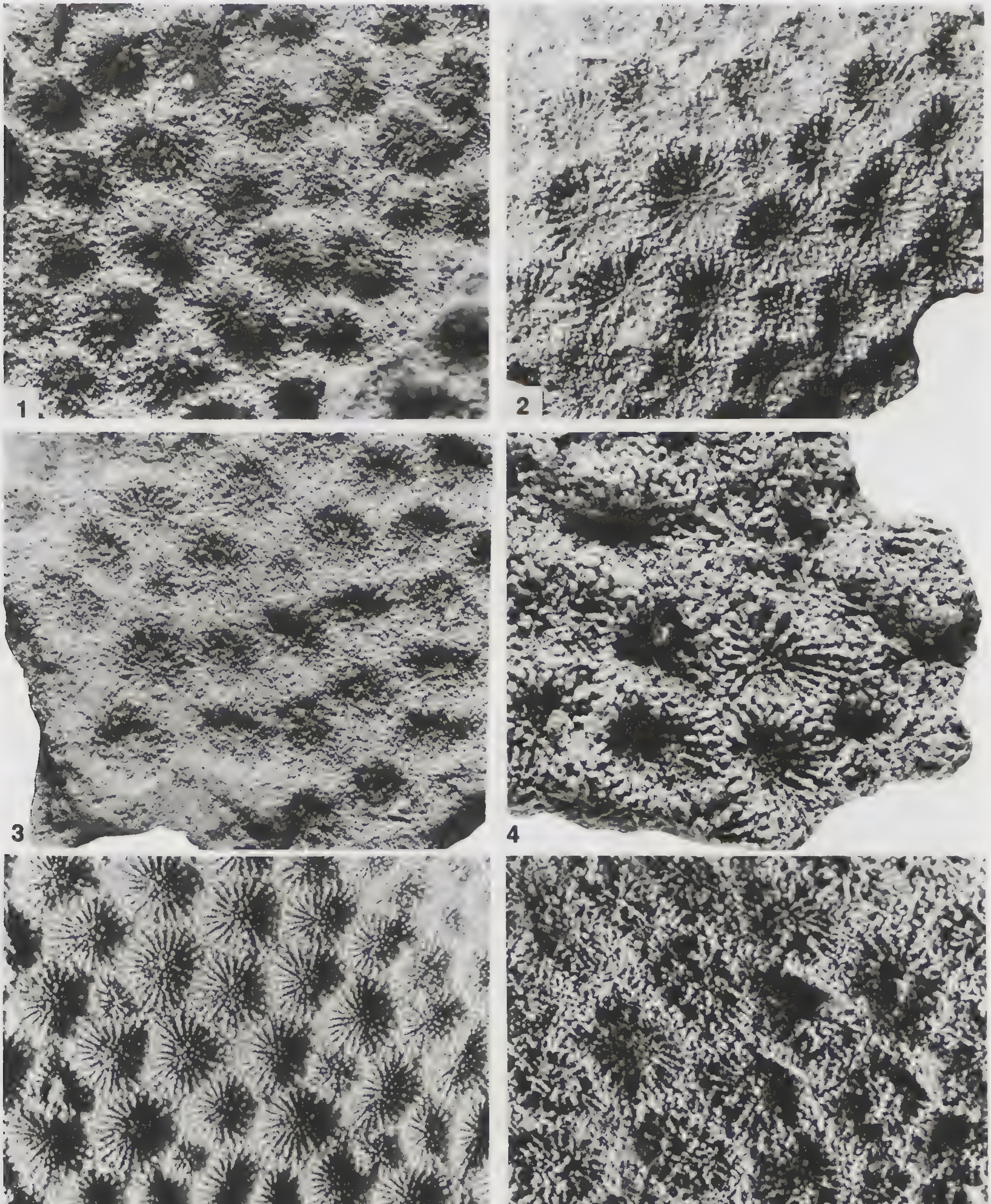
EXPLANATION OF PLATE 33

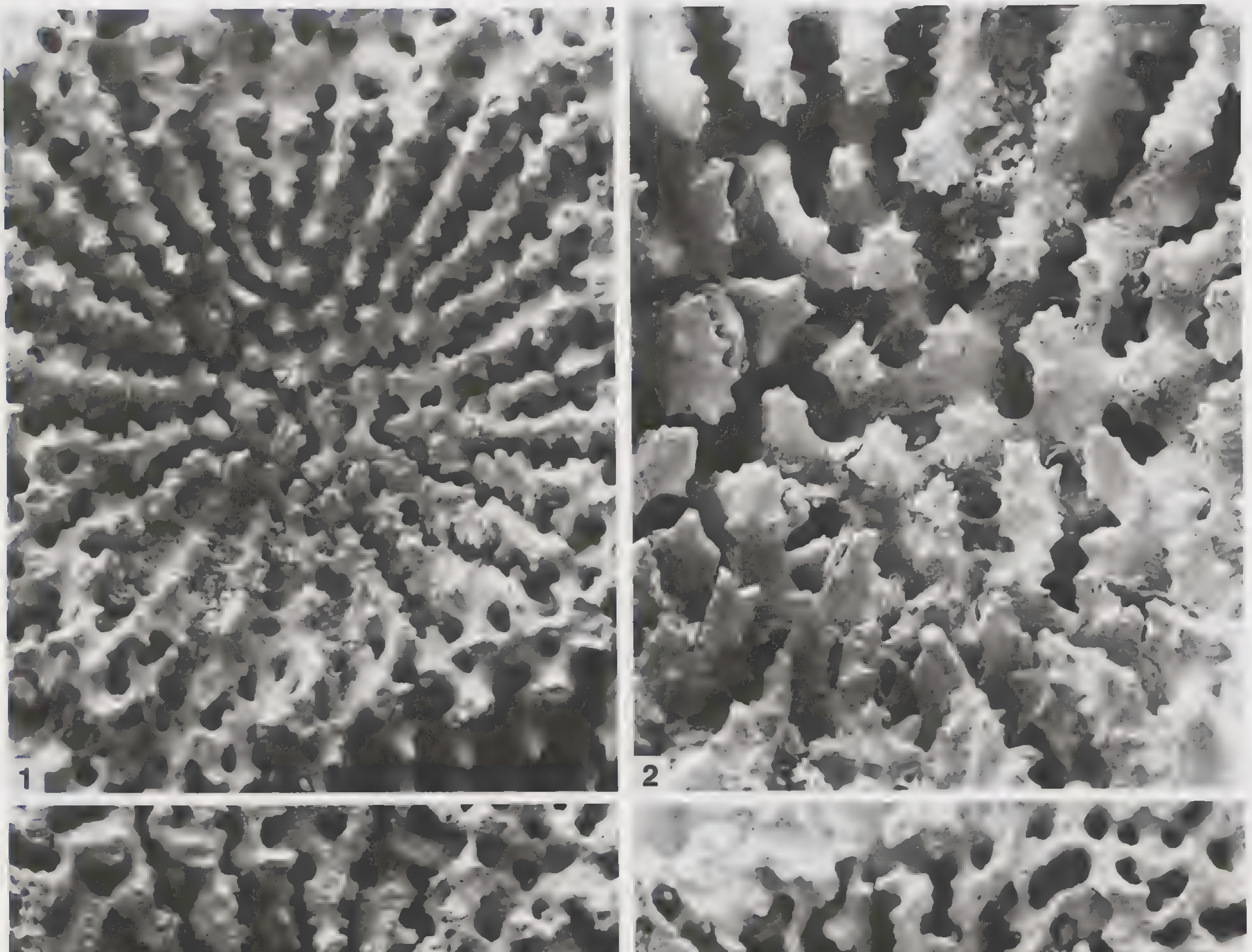
Page
Goniopora hilli Vaughan 83

Close-ups of calical surfaces. Calices are highly-elevated, large, and separated by a relatively-reduced mural reticulum of variable thickness. The columella tangle and pali are poorly-developed; therefore, the fossa is characteristically V-shaped.

Figure

1. Holotype. USNM 325058.
   Same specimen as Plate 32, figure 1. Calical surface, ×5.
2. Figured Specimen. USNM 68317.
   Same specimen as Plate 32, figure 3. Calical surface, ×5.
3. Figured Specimen. USNM 72891.
   Middle Miocene, USGS locality 6016, La Boca Formation, Panama. Calical surface, ×5 (lectotype of *Goniopora canalis* Vaughan).
4. Figured Specimen. USNM 325081.
   Lower Miocene, USGS locality 6775, White Springs, Florida. Calical surface, ×5 (paratype of *Goniopora jacobiana* Vaughan).
5. Figured Specimen. NMB D5853.
   Same specimen as Plate 32, figure 4. Calical surface, ×5.
6. Figured Specimen. NMB D5855.
   Same specimen as Plate 32, figure 6. Calical surface, ×5.

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EXPLANATION OF PLATE 34

Page

Goniopora hilli Vaughan 83

SEM photographs of calices. The columella structure is reduced, and the septa extend almost completely to the calice center. The pali are weakly-developed. The septa are thick with prominent denticles.

Figure

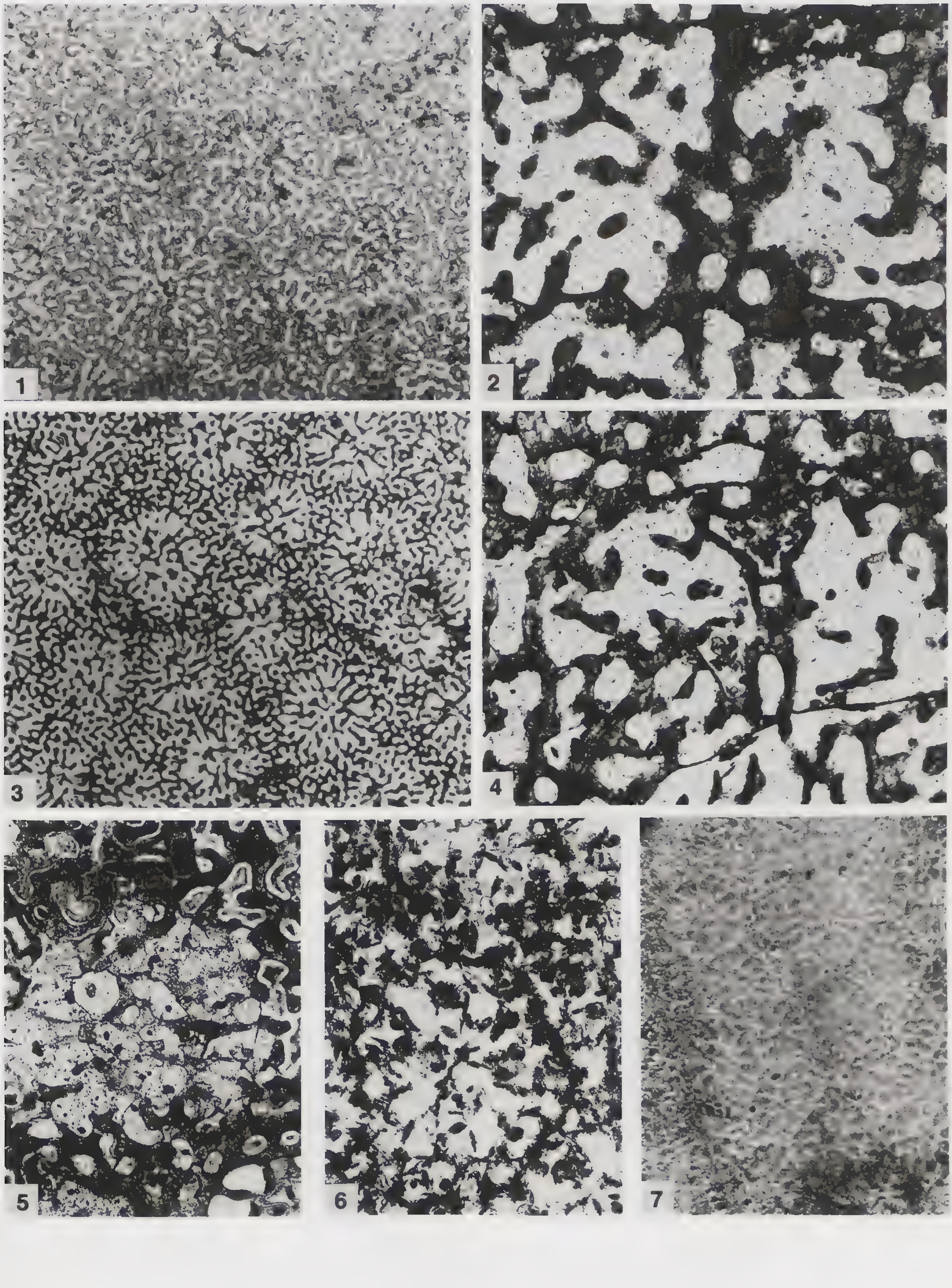
1. Figured Specimen. NMB D5853.
   Same specimen as Plate 32, figure 4 and Plate 33, figure 5, ×28.
2. Figured Specimen. NMB D5853.
   Same specimen as figure 1 above, ×67.
3. Figured Specimen. NMB D5854.
   Same specimen as Plate 32, figure 5, ×28.
4. Figured Specimen. NMB D5856.
   Lower Pliocene, NMB locality 16818, Río Cana, Gurabo Formation, Dominican Republic, ×28.

EXPLANATION OF PLATE 35

Goniopora hilli Vaughan and ***Goniopora imperatoris*** Vaughan. Thin-sections. Corallites of *G. hilli* appear larger with thick septa and indistinct, irregular columellae; whereas in *G. imperatoris,* the septa are narrow with prominent pali, thick columella tangles, and a pronounced, well-developed coenosteal reticulum.

Figure Page

1. ***G. hilli,*** Figured Specimen. NMB D5854 83
   Same specimen as Plate 32, figure 5. Transverse thin-section, ×5.
2. ***G. hilli,*** Figured Specimen. NMB D5856 83
   Same specimen as Plate 34, figure 4. Longitudinal thin-section, ×25, showing columella (center), dissepiments, and synapticulae.
3. ***G. imperatoris,*** Figured Specimen. NMB D5862 85
   Upper Miocene, NMB locality 16853, Río Cana, Cercado Formation, Dominican Republic. Transverse thin-section, ×5.
4. ***G. imperatoris,*** Figured Specimen. NMB D5858 85
   Upper Miocene, NMB locality 16856, Río Cana, Cercado Formation, Dominican Republic. Longitudinal thin-section, ×25, showing mural trabeculae (right), columella (left center), dissepiments and synapticulae.
5. ***G. imperatoris,*** Figured Specimen. BM(NH) R28678 85
   Upper Oligocene, chert and marl of Antigua. Transverse thin-section, ×25 (holotype of *Alveopora daedalaea regularis* Duncan).
6. ?***G. imperatoris,*** Figured Specimen. BM(NH) R28702 86
   Upper Oligocene, marl of Antigua. Transverse thin-section, ×25 (holotype of *Alveopora daedalaea minor* Duncan).
7. ?***G. imperatoris,*** Figured Specimen. BM(NH) R28625 86
   Upper Oligocene, marl of Antigua. Polished surface, ×10 (holotype of *Alveopora microscopica* Duncan).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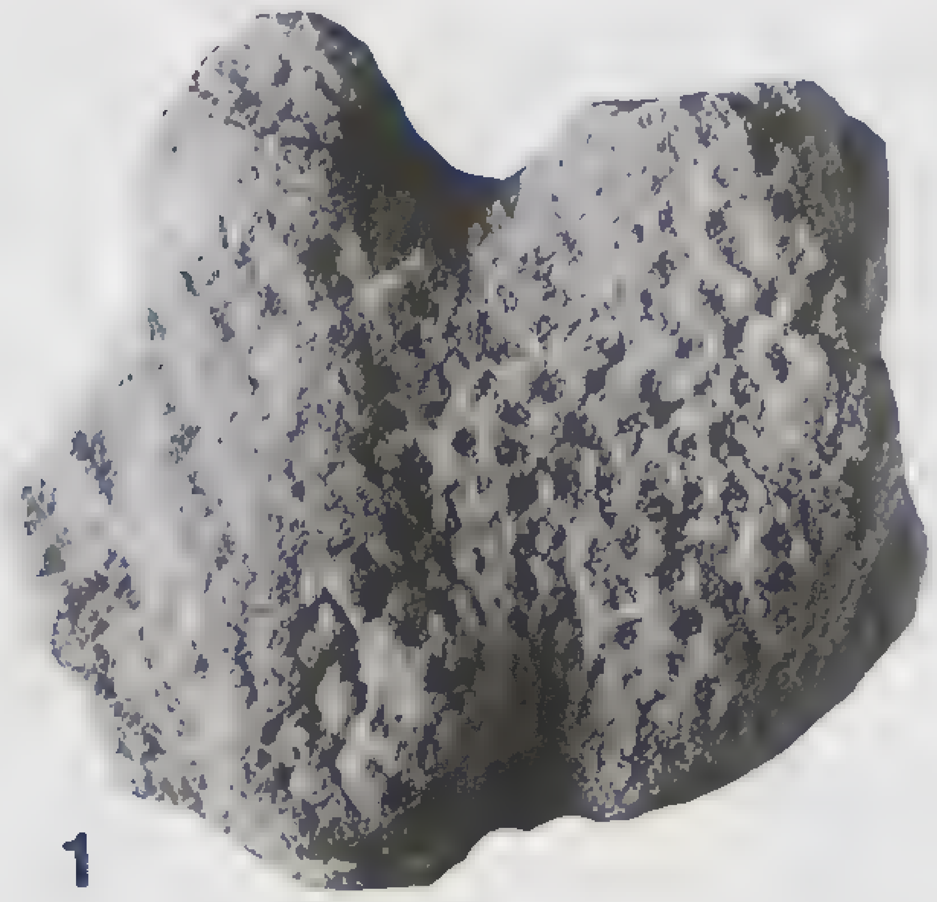
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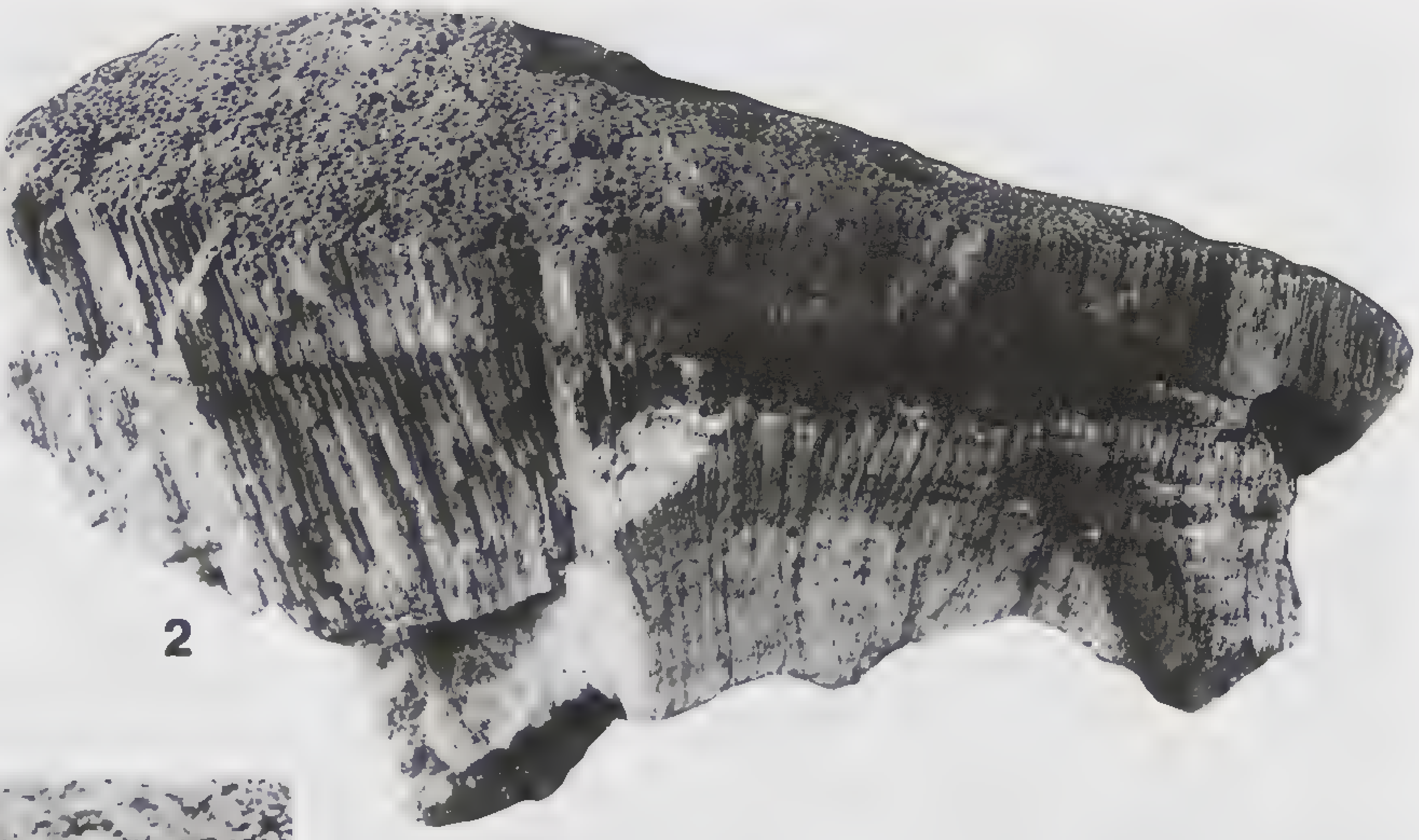
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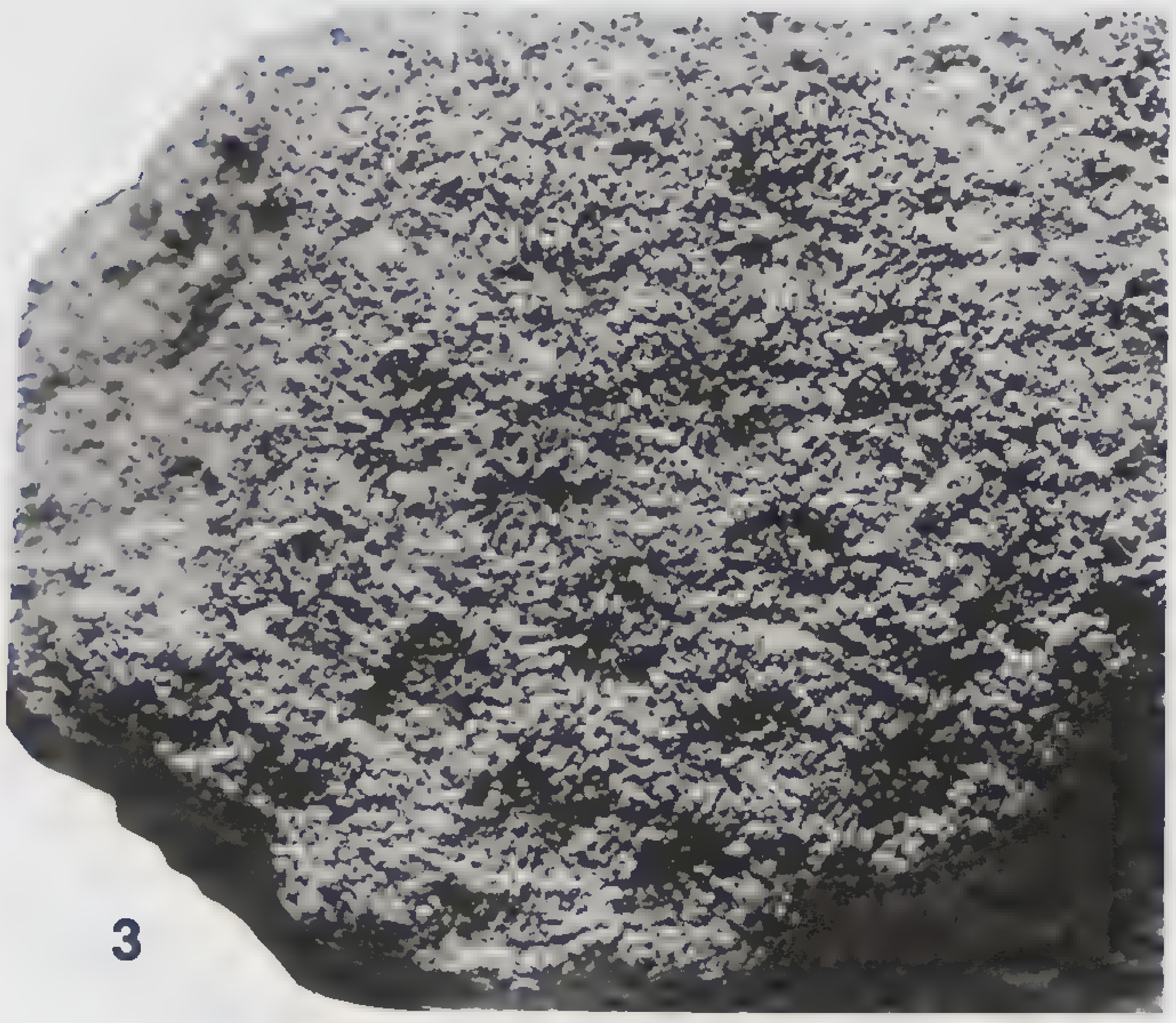
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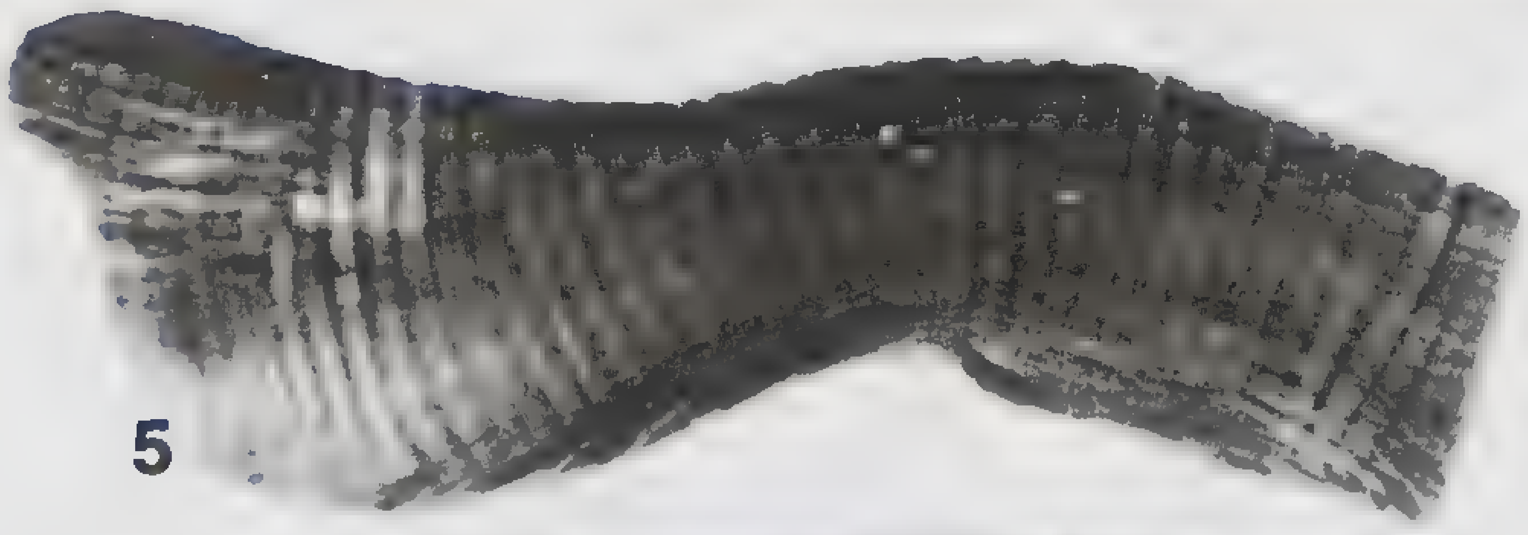
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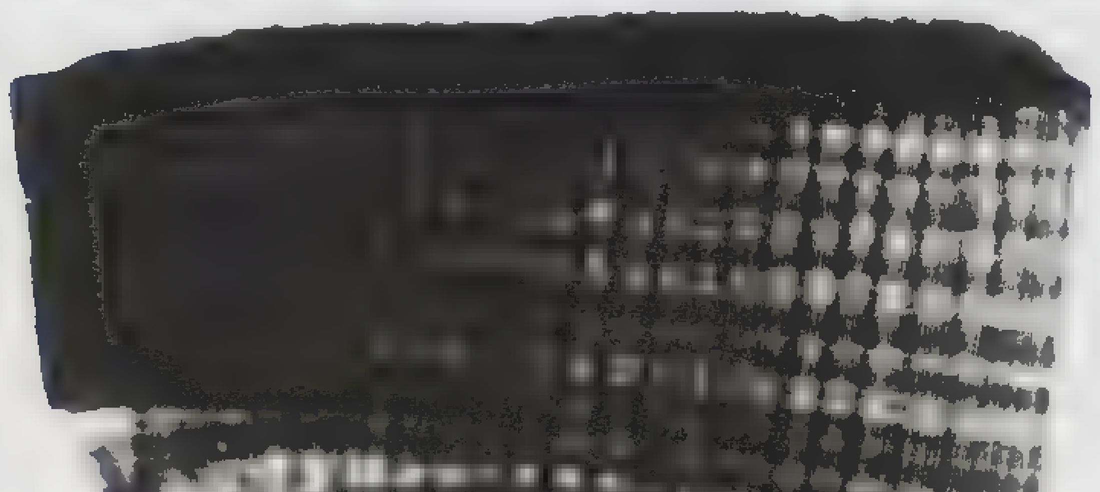
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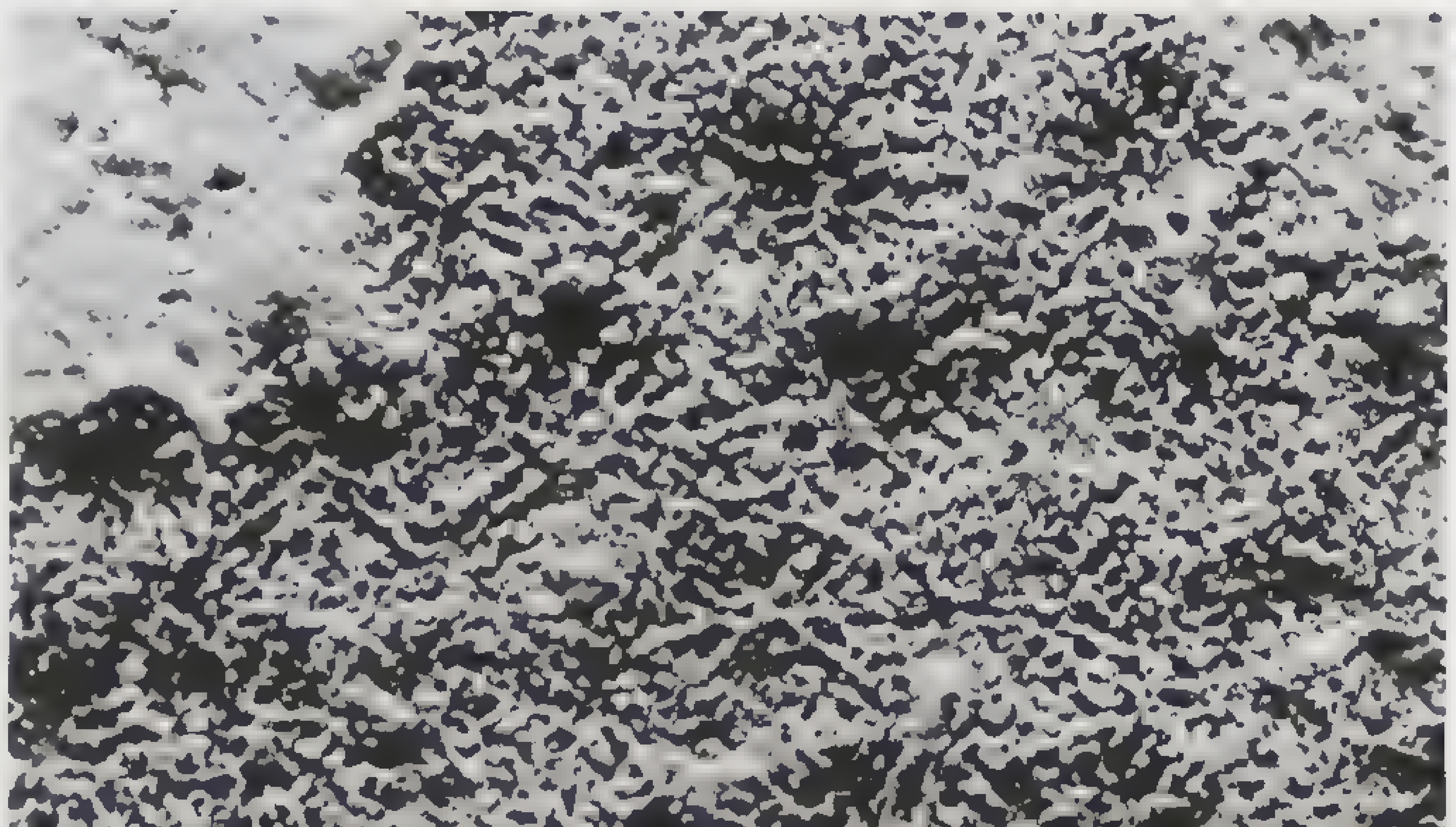
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EXPLANATION OF PLATE 36

Page

Goniopora imperatoris Vaughan 85

Whole colonies, close-ups of calical surfaces, and X-radiographs of colonies. Like *G. hilli,* colonies form large, smooth, well-rounded mounds with growth bands at intervals of 3 to 4 mm. However, corallites are smaller and the coenosteal reticulum more pronounced.

Figure

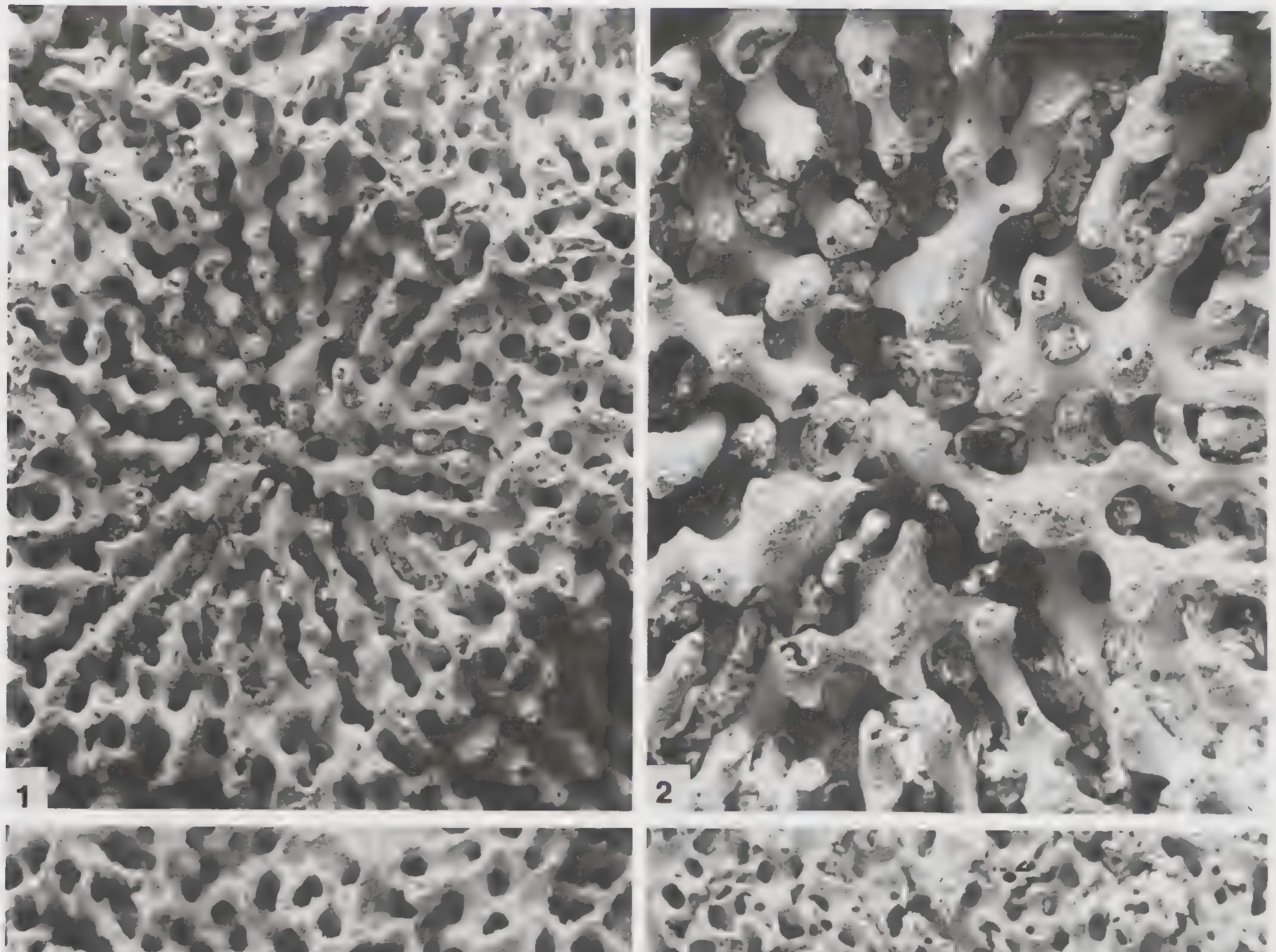
1. Holotype. USNM 325049.
   Middle Miocene, USGS locality 6016, La Boca Formation, Panama. Upper colony surface, ×1.
2. Figured Specimen. NMB D5859.
   Upper Miocene, NMB locality 16853, Río Cana, Cercado Formation, Dominican Republic. Side view of colony, ×¼.
3. Holotype. USNM 325049.
   Same specimen as figure 1 above. Calical surface, ×5.
4. Figured Specimen. NMB D5859.
   Same specimen as figure 2 above. Calical surface, ×5.
5. Figured Specimen. NMB D5858.
   Same specimen as Plate 35, figure 4. X-radiograph, ×1.
6. Figured Specimen. NMB D5862.
   Same specimen as Plate 35, figure 3. X-radiograph, ×1.
7. Possible synonym, holotype of *Goniopora decaturensis silicensis* Vaughan. USNM 325026.
   Lower Miocene, USGS locality 3381, Chattahoochee Formation, Georgia. Calical surface, ×5.

EXPLANATION OF PLATE 37

Page
Goniopora imperatoris Vaughan 85

SEM photographs of calices. Corallites have numerous thin septa that extend to a well-developed columella tangle defined by several rows of synapticulae.

Figure
1. Figured Specimen. NMB D5862.
   Same specimen as Plate 35, figure 3 and Plate 36, figure 6, ×28.
2. Figured Specimen. NMB D5862.
   Same specimen as figure 1 above, ×67.
3. Figured Specimen. NMB D5858.
   Same specimen as Plate 36, figure 5, ×28.
4. Figured Specimen. NMB D5861.
   Lower Miocene, NMB locality 16944, Río Yaque del Norte, Baitoa Formation, Dominican Republic, ×28.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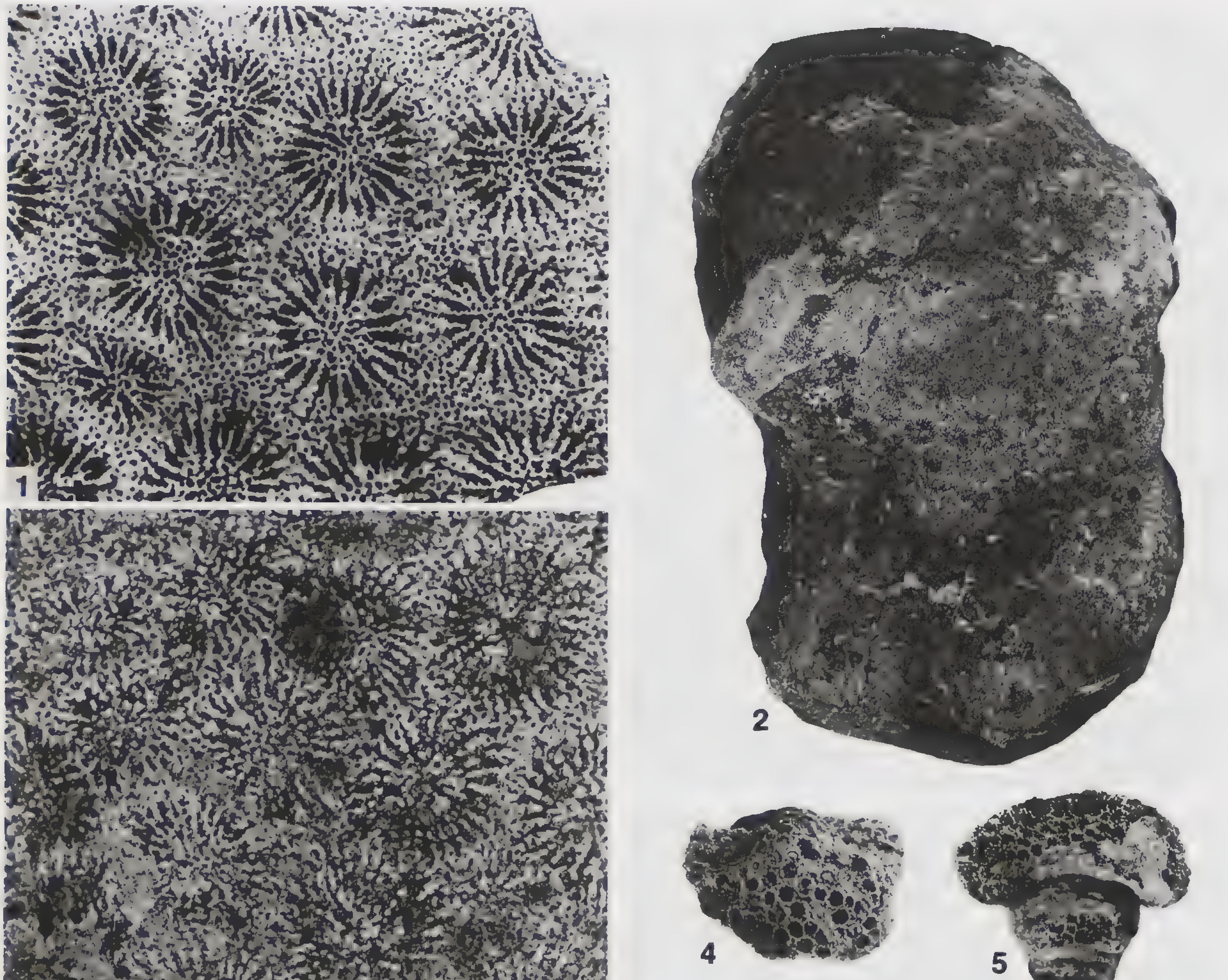
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EXPLANATION OF PLATE 38

Goniopora calhounensis Weisbord and ***Alveopora tampae*** Weisbord. Whole colonies and close-ups of calical surfaces. Calices of *G. calhounensis* are notably large with a thick coenosteal reticulum, well-developed pali and thick synapticulae. The *Alveopora* has characteristic thecal pores and irregular septal spines.

Figure	Page
1. ***G. calhounensis***, Holotype. FSU CH3-3a Middle Miocene, Chipola Formation, Florida. Calical surface, ×5.	87
2. ***G. calhounensis***, Figured Specimen. NMB D5863 Upper Miocene, NMB locality 16921, Río Gurabo, Gurabo Formation, Dominican Republic. Side view of colony, ×1.	87
3. ***G. calhounensis***, Figured Specimen. NMB D5863 Same specimen as figure 2 above. Calical surface, ×5.	87
4. ***A. tampae***, Topotype. USNM 66225 Lower Miocene, USGS locality 2084, Ballast Point, Tampa Formation, Florida. Side view of colony, ×1.	88
5. ***A. tampae***, Topotype. USNM 66224 Lower Miocene, USGS locality 2115, Hillsborough Bay, Tampa Formation, Florida. Side view of colony, ×1.	88
6. ***A. tampae***, Topotype. USNM 66224 Same specimen as figure 5 above. Calical surface, ×5.	88
7. ***A. tampae***, Figured Specimen. USNM 63253 Upper Oligocene USGS locality 8713, El Limon, Tabera Group, Dominican Republic. Colony surface, ×5.	88

INDEX

Note: Page numbers are in light face, plate numbers are in **bold face** type; principal discussion pages are in *italics.*

Agaricia dominicensis Vaughan, 1919 49
Almy and Carrión-Torres (1963) 56
Alveopora Blainville, 1830 .... 48,50,52,59,71,74,*88*
chiapanecae Frost and Langenheim, 1974 88
daedalaea var. *minor* Duncan, 1863 86
daedalaea var. *regularis* Duncan, 1863 86
fenestrata (Lamarck) Dana, 1846 48,79
fenestrata (Dana) of Duncan, 1863 74,79,81
microscopica Duncan, 1863 86
tampae Weisbord, 1973 .... **38** 52,53,74,*88*
?*Alveopora daedalea* var. *regularis* Duncan, 1863 85
AMNH (American Museum of Natural History, New York, NY, U.S.A.) 49,76,81,82,85,87
Anguilla 60,74,79,81,85,87
Crocus Bay 60
Anguilla Formation 79,81,85,87
anguillensis,
Porites 60,74,79,82
?*Porites* 78
ANSP (Academy of Natural Sciences, Philadelphia, PA, U.S.A.) 48,49,87
Antigua 74,81,84,86,87
Antigua Formation 81,87
Antilles 62
Antillocyathus Wells, 1937 49
Aspidosiphon corallicola Sluiter, 1889 77
astreoides, Porites .... **15** *56*,58,62,73,78,79,80,82,83
astreoides braziliensis, Porites 62
aucillana, Goniopora 59,74,83,84
Australia 59,83,88
Austria, Niederleis near Enzefeld 62

Bahns, T. 49
Baitoa Formation 52,81,83,85–87
ballistensis, Goniopora 60,74,79,81
baracoaensis, Porites .... **16,17,18** 50,51,52,53,54, 55,60,64,66,67,68,69,70,71,73,74,*75*,76,81,89
baracoaensis matanzasensis, Porites 60
Baracoa Formation 76
baracoäensis, Porites 75
baracoäensis var. *matanzaensis, Porites* 75
Barta-Calmus, S. 49
Bernard (1900) 59
Bernard (1901) 56
Bernard (1903) 56,59,60,74,75,82,83
Bernard (1905) 56,59,60,63,74,75,82
Bernard (1906) 59,82
Bernoulli, D. 49
Best, M. B. 49
Binomial statistical test 53
Blainville (1830) 83,88
BMDP program 2M 63
BMDP program 7M 63,68
BM(NH) (British Museum [Natural History], London, England, U.K.) 48,49,81,82
Bold (1966) 74
Bold (1970) 74
Bold (1975) 74
Bowden Formation 76
Box's test 68
Brakel (1976) 56,59
Brakel (1977) 58
branneri, Porites .... **15** *56*,62,73,77,83
Brazil 56,73,75
Abrolhos Archipelago 62
Abrolhos Reefs 62
Fernando de Novonha Is. 62
Parahyba do Norte 62
Pernambuco,
Canderas Reef 62
Farinha, Maria 62
Recife Military Air Base 62

Cairns, S. D. 49
Cairns (1982) 56
calabricae, Porites 62,83
calhounensis, Goniopora .... **38** 52,53,59,65,69, 70,74,86,*87*,88,89
California, San Diego Co., Barrett Canyon 60
Caloosahatchee Formation 71
canalis, Goniopora 60,74,83,84,85
carrizensis, Porites 60,74
cascadensis, Goniopora 60,74,79,80,81
Cercado Formation 52,76,77,81,83,87
Chattahoochee Formation 86,87
Cheetham, A. H. 49
Chevalier collections 49
Chevalier (1961) 62,71,76,77,83,85,88
chiapanecae, Alveopora 88
Chipola Formation 85–88
chipolanum, Porites 59,74,76
Christen, H. 49
Cisne and Rabe (1978) 56
clavaria, Porites 62,71
clevei, Goniopora 60,74,79,80,81
cochlea, Heteropsammia 77
Cock (1977) 56
collegniana, Porites 48,62,77,81
compressa, Porites 58
convivatoris, Porites .... **19,20** 47,50,51,52,53,54,55,64, 66,67,68,69,70,71,73,74,*76*,77,89
Cooke, W. 49
copoyensis, Goniopora 87
corallicola, Aspidosiphon 77
Corallium, poris stellatis of Seba, 1756 75
Cornelius, P. 49
Coryell and Ohlsen (1929) 74,76,81,82,85,86
Cosmoporites Duchassaing and Michelotti, 1866 75
Crimea 83
Cuba 74,76,85
Baracoa 60,75
La Cruz 60
Matanzas 60
Curaçao 75
Cuvier (1798) 75

daedalaea var. *minor, Alveopora* 86
daedalaea var. *regularis, Alveopora* 86

daedalea, Madrepora 85,88
daedalea var. *regularis, Alveopora* 85
Dana (1846) 48,58,74
decaturensis,
  Goniopora 60,74,86
  ?Goniopora 84,85
decaturensis var. *bainbridgensis,*
  Goniopora 86
  ?Goniopora 85
decaturensis var. *silicensis,*
  Goniopora 86
  ?Goniopora 85
divaricata, Porites **15** *56*,62,73,77
Dixon (1981) 63
Dogan, U. 49
Dominican Republic,
  Arroyo Puñal 50
  Baitoa 50
  Bulla 50
  Cañada Zalaya 50
  Cibao Valley region 47,48,50,53
  city of Santiago 50
  Esperanza 50
  Guayubin 50
  Janico 50
  Los Quemados 50
  Moca 50
  Moncion 50
  Navarrete 50
  Río Amina 49,50
  Río Cana 49,50,52–54,76,77,79,81,83,85,87,88
  Río Guayubin 50
  Río Gurabo 49,50,52–54,76,79,81,83,85,88
  Río Mao 49,50,53,74,76,77,79,81,87
  Río Verde 50
  Río Yaque del Norte 49,50,52,53,81,83,85–87
  Angostura Gorge 52
  Arroyo López section 52
  Santiago Rodriguez 50
  Valverde (Mao) 50
  Zamba 50
dominicensis,
  Agaricia 49
  Porites 77
douvillei,
  Porites 60,74,76,81,82
  ?Porites 75
Druecker, T. 49
Dry Tortugas 62
Duchassaing and Michelotti (1866) 75
Düggelin, M. 49
Duncan (1863) 48,74,81,84–87
Duncan (1864) 48
Duncan (1868) 48
Durham (1947) 73

Eggenburg Museum, Maïgen near Eggenburg, Austria 62
Eldredge, N. 49
Elter, O. 49
Eng, R. C. 49
Esper collection 62

fenestrata, Alveopora 48,79
Florida 71,74,81,83,85,86,88
  Calhoun Co., Tenmile Creek 87
  Pulaski Bay 62
  Tampa 60,84
    Ballast Point 82
    Hillsborough Bay 88
  White Springs 60
Florida Keys 62
Forskål (1775) 85,88
Foster (1979) 58
Foster (1980) 58
Foster (1984) 63,70
Foster (1985) 59
Foster (in preparation) 71
France,
  Aquitaine,
    Manciet 62
    Mérignac 62
    Peyrère de Peyrehorade 62
    St. Paul-Les-Dax 62,88
    Villandraut 62
  Touraine, Pontlevoy 62
Frost (1977a) 48
Frost (1977b) 48
Frost (1977c) 71
Frost and Langenheim (1974) 74,76,79,81,82,85–88
Frost *et al.* (1983) 74
FSU (Florida State University, Department of Geology, Tallahassee, FL, U.S.A.) 49,50,59,76,84,87
furcata, Porites 48,56,62,73,76
furcata var. 2, *Porites* **15** *62*

Gabb, W. B. 48
Gabb collection 49
Gabb (1873) 48
Geister, J. 48,49,59
Geister (1983) 56,75
Georgia 74,87
  Decatur Co. 86
  Hales Landing 60
Globorotalia humerosa Zone 54
Globorotalia margaritae Zone 54
Globorotalia miocenica Zone 54
globulosa, Goniopora 62,88
Golden, J. 49
Goniopora Blainville, 1830 47,48,50,52,53,57,59, 60–63,65–72,75,80,*83*,84–87,89,90
  aucillana Weisbord, 1973 59,74,83,84
  ballistensis Weisbord, 1973 60,74,79,81
  calhounensis of Vaughan 86
  calhounensis Weisbord, 1971 **38** 52,53,59,65,69, 70,74,86,*87*,88,89
  canalis Vaughan, 1919 60,74,83,84,85
  cascadensis Vaughan, 1919 60,74,79,80,81
  clevei Vaughan, 1919 60,74,79,80,81
  copoyensis Frost and Langenheim, 1974 87
  decaturensis Vaughan, 1919 60,74,86
  decaturensis var. *bainbridgensis* Vaughan, 1919 86
  decaturensis var. *silicensis* Vaughan, 1919 86
  globulosa Chevalier, 1961 62,88
  granosa Chevalier, 1961 62
  hilli Vaughan, 1919 **32,33,34,35** 50,51,52,53, 57,60,65,67,69,70,71,74, *83*,84,85,86,87,89
  imperatoris Vaughan, 1919 **35,36,37** 50,51,52,53,57,60,65, 67,69,70,74,84,*85*,86,87,89

Goniopora
jacobiana Vaughan, 1919 60,74,83,84,85
matsoni Weisbord, 1973 60,74,79,81
microscopica (Duncan, 1863) 87
panamensis Vaughan, 1919 60,74,84,85
pendunculata Quoy and Gaimard *in* Blainville, 1830 83
portoricensis Vaughan, 1919 60,79
regularis (Duncan, 1863) 86
taberi Wells, 1934 87
tampaensis Weisbord, 1973 60,74,83,84
turonensis Chevalier, 1961 62,71,85
"*Goniopora calhounensis*" 87
"*Goniopora daxitertia Bernard*" of Chevalier, 1961 88
?*Goniopora*,
decaturensis Vaughan, 1919 84,85
decaturensis var. *bainbridgensis* Vaughan, 1919 85
decaturensis var. *silicensis* Vaughan, 1919 85
Goreau (1959) 75
Goreau, Goreau, and Hayes (1981) 58
Goreau and Wells (1967) 75
Goreau and Yonge (1968) 77
granosa, Goniopora 62
Grasshoff, M. 49
Gray (1842) 74
Great Barrier Reef 77
Groot, G. E. de 49
Guggenheim, R. 49
Gurabo Formation 52,76,77,79,81,83,85,87,88

Hartman, W. D. 49
Hawaii 58,88
Heneken collection 48
Heneken (1853) 48
Heteropsammia cochlea (Spengler, 1781) 77
hilli, Goniopora ...... **32,33,34,35** 50,51,52,53,57,60,65,67, 69,70,71,74,*83*,84,85,86,87,89
howei,
Porites 74,80,81
Porites (Synaraea) 60
?*Porites (Synaraea)* 79
Hungary, Forchtenau 62,

imperatoris, Goniopora .... **35,36,37** 50,51,52,53, 57,60,65,67,69,70,74,84,*85*,86,87,89
incrustans, Porites 62,71,77
Indian Ocean 83
Indonesia 83,88
Institute de Paléontologie, Paris, France 49
irregularis, Rhodaraea 84
Italy,
Calabria, Vibo Valentia 62
Livorno, Popogna 62

jacobiana, Goniopora 60,74,83,84,85
Jamaica 74,76
Discovery Bay 56,58,78,80
Johnson, L. 49
Jones, C. C. 49
Jung, P. 47–49,59
Jung (1986) 73

Klapper, G. 49
Klapper, J. 49
Kojis and Quinn (1982) 58
Kruskal–Wallis test 53
Kühn (1925) 62,71,83

La Boca Formation 75,76,79–83,85,87
Emperador Limestone Member 78,84,86
La Cruz (Marl) Formation 76,85
La Quinta Formation 76,79,81,83,85–87
Laborel collection 62
Laborel (1969) 56
Lamarck collection 49,62
Lamarck (1816) 48,56,58,62,71,73,76,79,80,82,83
Langenheim, R. L., Jr. 49,85
Lares (Limestone) Formation 76,80,81,83,85
leptoclada, Porites 62,71,77
Leseuer (1821) 56,62,73,77
Levene's test 69
Link (1807) 75
lobatosepta, Porites 62,71,77
Lüönd, G. 49

macdonaldi,
Porites .... **21,22,23** 50,51,52,53,54,55,64,66,67, 68,69,70,71,73,74,*78*,79,81,83,89
Porites (Synaraea) 60,78,79
Madagascar 88
Madrepora daedalea Forskål, 1775 85,88
Madrepora porites Pallas, 1766 75
maïgensis, Porites 62,71,83
Maldives 88
mancietensis, Porites 62,71,76
Mao Formation 52,76,79,81,83,87,88
Maréchal, J. 49
matsoni, Goniopora 60,74,79,81
Maury collection 49
Maury (1917) 49
Maury (1919) 74
mauryi, Porites 76
MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.) 48–50
Mers d'Amérique 62
Messinian salinity crisis 83
Mexico, Chiapas 74,76,79,81,83,85,86,87
MHNP (Muséum National d'Histoire naturelle, Paris, France) 49,50,62
Michelin (1842) 48,62,77,81
Micronesia 88
microscopica,
Alveopora 86
Goniopora 87
Miller (1968) 68
Milne-Edwards and Haime (1851) 62,71,77
Montastraea Blainville, 1830 58,70,71
Moser, H. 49
Müller, K. 49
Museo di Zoologia Sistematica, Torino, Italy 49

National Science Foundation (Switzerland) 49
National Science Foundation (U.S.A.) 49
Natur-Museum Senckenberg, Frankfurt, West Germany 49,62
Neoporites Duchassaing and Michelotti, 1866 75
New Guinea, Port Dorey 83
NHMW (Naturhistorisches Museum Wien, Vienna, Austria) 49,50,62
"Nivajé Shale" 48

NMB (Naturhistorisches Museum Basel, Basel, Switzerland) 47,49,50,52,59,62,64–67,72,74,76,77,79,81,82,83,85,87
NMB loc. 15806 76
NMB loc. 15808 76,81,85
NMB loc. 15814 76
NMB loc. 15821 81
NMB loc. 15822 76,81
NMB loc. 15824 76,79,81
NMB loc. 15826 76,79,81,83
NMB loc. 15830 76
NMB loc. 15834 76,81
NMB loc. 15837 76,79,81,85
NMB loc. 15838 76,81
NMB loc. 15839 76
NMB loc. 15840 76,81
NMB loc. 15841 79
NMB loc. 15842 76
NMB loc. 15844 76
NMB loc. 15845 76,81
NMB loc. 15846 76,79,83
NMB loc. 15849 76,81
NMB loc. 15850 76,81
NMB loc. 15851 76,79,81
NMB loc. 15852 79
NMB loc. 15853 76,81
NMB loc. 15855 79,81
NMB loc. 15856 76
NMB loc. 15857 79
NMB loc. 15858 76
NMB loc. 15859 76
NMB loc. 15861 85
NMB loc. 15862 76
NMB loc. 15863 76
NMB loc. 15878 83
NMB loc. 15884 85
NMB loc. 15887 83
NMB loc. 15893 81
NMB loc. 16122 76
NMB loc. 16184 81
NMB loc. 16811 76,79,81,83
NMB loc. 16815 79,81
NMB loc. 16817 83
NMB loc. 16818 85,87
NMB loc. 16819 83
NMB loc. 16823 79,81,83
NMB loc. 16826 76,79,81
NMB loc. 16836 77
NMB loc. 16839 77
NMB loc. 16844 77
NMB loc. 16852 77
NMB loc. 16853 76,81,83,87
NMB loc. 16855 83
NMB loc. 16856 76,81,83,87
NMB loc. 16861 76,79
NMB loc. 16863 76
NMB loc. 16875 88
NMB loc. 16876 87
NMB loc. 16879 77
NMB loc. 16881 76,79,81,83
NMB loc. 16882 76,79,81
NMB loc. 16883 76,79,81
NMB loc. 16884 76,81
NMB loc. 16885 76,81,83
NMB loc. 16909 81
NMB loc. 16911 76,79,81,87
NMB loc. 16913 77
NMB loc. 16915 77
NMB loc. 16916 77
NMB loc. 16918 77
NMB loc. 16921 76,79,81,85,88
NMB loc. 16922 77
NMB loc. 16926 77
NMB loc. 16928 52,77
NMB loc. 16929 77
NMB loc. 16933 79,81,83,85
NMB loc. 16934 76,81
NMB loc. 16936 83
NMB loc. 16937 85
NMB loc. 16939 87
NMB loc. 16943 83,85
NMB loc. 16944 85,87
NMB loc. 16984 77
NMB loc. 16986 77
NMB loc. 17004 76
NMB loc. 17272 83
NMB loc. 17273 83
NMB loc. 17275 83
NMB loc. 17277 81,83
NMB loc. 17279 81
NMB loc. 17283 85
NMB loc. 17284 83,85,87
NMB loc. 17289 83

pachysepta, Porites 62,83
Pallas (1766) 56,62,71,75–77
Panama 74–76,79–81,83,85,87
Panama Canal Zone,
  Empire Quarry 60,78,82,84,86
  Las Cascadas 60
panamensis,
  Goniopora 60,74,84,85
  Porites 60,81,82,86
Panchaud, R. 49
pendunculata, Goniopora 83
Petrick, R. 49
Pielou (1969) 53
PIU (Paleontologiska Institutionen Uppsala, Uppsala, Sweden) 50,60,79
polymorphus, Porites 75
Ponce Formation 81,83,85–87
Porites Cuvier, 1798 75
Porites Link, 1807 .... 47,48,50,52–56,58–63, 66–73,*75*,77,80–83,89,90
  anguillensis Vaughan, 1919 60,74,79,82
  astreoides Lamarck, 1816 .... **15** *56*,58,62,73,78, 79,80,82,83
  astreoides Lamarck of Coryell and Ohlsen, 1929 74,82
  astreoides braziliensis Verrill, 1901a 62
  baracoaensis Vaughan, 1919 ... **16,17,18** 50,51,52,53,54, 55,60,64,66,67,68,69,70,71,73,74,*75*,76,81,89
  baracoaensis matanzasensis Vaughan, 1919 60
  baracoäensis Vaughan, 1919 75
  baracoäensis var. *matanzaensis* Vaughan, 1919 75
  branneri Rathbun, 1887 .... **15** *56*,62,73,77,83
  calabricae Chevalier, 1961 62,83
  carrizensis Vaughan, 1917 60,74
  chipolanum Weisbord, 1971 59,74,76
  clavaria Lamarck, 1816 62,71

Porites
collegniana Michelin, 1842 48,62,77,81
collegniana Michelin of Duncan, 1863 74,81
compressa Dana, 1846 58
convivatoris, n. sp. .... **19,20** 47,50,51,52,53,54,55,64,66, 67,68,69,70,71,73,74,*76*,77,89
divaricata Leseuer, 1821 .... **15** *56*,62,73,77
dominicensis 77
douvillei Vaughan, 1919 60,74,76,81,82
furcata Lamarck, 1816 48,56,62,73,76
furcata var. 2 of Lamarck, 1816 .... **15** *62*
howei Vaughan, 1919 74,80,81
incrustans Milne-Edwards and Haime, 1851 62,71,77
leptoclada Reuss, 1872 62,71,77
lobatosepta Chevalier, 1961 62,71,77
macdonaldi Vaughan, 1919 .... **21,22,23** 50,51,52,53, 54,55,64,66,67, 68,69,70,71,73,74, *78*,79,81,83,89
maïgensis Kühn, 1925 62,71,83
mancietensis Chevalier, 1961 62,71,76
mauryi 76
pachysepta Chevalier, 1961 62,83
panamensis Verrill, 1866 81,82
panamensis Vaughan, 1919 60,81,82,86
polymorphus Link, 1807 75
porites (Pallas, 1766) .... **15** *56*,62,71,73,75,76,77
portoricensis (Vaughan, 1919) .... **24,25,26,27,28** 50,51,52,53, 54,55,64,66,67,68,69,70,71,73,74,76,*79*,80,81,83,89
toulai Vaughan, 1919 60,74,75,76,81
trinitatis Vaughan, *in* Vaughan and Hoffmeister, 1926 60,74,82
verrilli Rehberg, 1893 .... **15** 62,73,83
waylandi, nom. nov. .... **29,30,31** 50,51,52,53,54, 55,64,66,67,68,69,70,71,73,74,79,*81*,82,83,89
porites,
Madrepora 75
Porites .... **15** *56*,62,71,73,75,76,77
Porites (Napopora) Quelch, 1884 74,78,79
Porites sensu stricto 79
Porites (Synaraea) Verrill, 1864 74,78
howei Vaughan, 1919 60
macdonaldi Vaughan, 1919 60,78,79
"*Porites floridaprima Bernard*" of Weisbord, 1973 .. 60,74,81,82
"*Porites willcoxi*" 82
?*Porites*,
anguillensis Vaughan, 1919 78
douvillei Vaughan, 1919 75
?*Porites (Synaraea) howei* Vaughan, 1919 79
portoricensis,
Goniopora 60,79
Porites .... **24,25,26,27,28** 50,51,52,53,54,55,64,66,67,68, 69,70,71,73,74,76,*79*,80,81,83,89
Pourtalès (1875) 48
PROC CORR 53
PROC REG 53
Puerto Rico 74,76,81–83,85,87
Guanica 82,85
Lares 60,80,82
Puri and Vernon (1964) 74

Quelch (1884) 74,78

Ramírez (1956) 49
Rathbun (1887) 56,62,73,77,83
Red Sea 83,88
regularis, Goniopora 86
Rehberg (1893) 62,73,83
Reuss (1872) 62,71,77
Rhodaraea irregularis Duncan, 1863 84
Ricart y Menéndez (1981a) 49
Ricart y Menéndez (1981b) 49
Ricart y Menéndez (1983) 49
Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands 49
Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands . 49
Río Lajas Formation 83
Roos (1967) 56
Roos (1971) 56
Rosen, B. R. 49
Runs statistical test 53
Rützler, K. 49

Samoa 88
Santa Ana Formation 81,83,86
SAS CANDISC procedure 67,68
SAS Inst. (1982) 53,67
SAS NPAR1WAY procedure 53
Saunders, J. B. 47–49,59,74
Saunders, Jung, and Biju-Duval (1986) 48,50,53,54, 56,59,74,77
Saunders *et al.* (1982) 48
Scherler, C. 49
Schmid, P. 49
Schultz, O. 49
Seba (1756) 75
Serrette, M. D. 49
Siderastraea Blainville, 1830 58
"Silt of the Sandstone plain" 48
Simpson diversity index 53
Sluiter, 1889 77
South China Sea 83
Spearman's rank order correlation coefficients 53
Spengler (1781) 77
SPSS Inc. (1983) 53
SPSS-X NPAR procedure 53
Stuenes, S. 49
SUI (State University of Iowa, Iowa City, IA, U.S.A.) 49,50, 58,68
Suter, W. 49
Suwannee Limestone 84,85

Tabera Group 52,54,81
taberi, Goniopora 87
tampae, Alveopora .... **38** 52,53,74,*88*
tampaensis, Goniopora 60,74,83,84
Tampa Formation 81,83–85,88
toulai, Porites 60,74,75,76,81
Trinidad 74
Cumuto Road 60
trinitatis, Porites 60,74,82
turonensis, Goniopora 62,71,85

UCMP (University of California Museum of Paleontology, Berkeley, CA, U.S.A.) 50,79
UI (University of Illinois, Urbana, IL, U.S.A.) 49,50,76, 81,82,85,86
Uppsala Universitet, Uppsala, Sweden 49

USGS (United States Geological Survey, Washington, DC, U.S.A.) 49,50,60
USGS loc. 2084 60
USGS loc. 2115 88
USGS loc. 3191 60,80
USGS loc. 3286 60,82
USGS loc. 3383 60
USGS loc. 3446 60
USGS loc. 3461 60
USGS loc. 3476 60,75
USGS loc. 6015 60,82
USGS loc. 6016 60,75,78,80,84,86
USGS loc. 6020c 60
USGS loc. 6546 60
USGS loc. 6775 60
USGS loc. 6893 60
USGS loc. 6966 60
USGS loc. 7616 60
USGS loc. 8299 60
USGS loc. 8668 86
USGS Library, Denver, CO, U.S.A. 77
USNM (United States National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.) 49,50,60, 62,75–82,84,86–88

Vaughan, T. W. 49,77
Vaughan collection 77,86
Vaughan (1901) 56,75
Vaughan (1907) 58
Vaughan (1917) 60,74
Vaughan (1919) 48–55,57,60,64–71,73–76,78–87
Vaughan (date unknown) 49,76
Vaughan and Hoffmeister (1925) 49
Vaughan and Hoffmeister (1926) 60,74,82
Vaughan and Wells (1943) 60,71,74,75
Vaughan *et al.* (1921) 49
Veron and Pichon (1982) 59,70,75,79,83,88
Verrill (1864) 74,78
Verrill (1866) 81,82
Verrill (1901a) 62
Verrill (1901b) 75
verrilli, Porites .... **15** *62*,73,83

waylandi, Porites .... **29,30,31** 50,51,52,53,54,55,64, 66,67,68,69,70,71,73,74,79,*81*,82,83,89
Weisbord collection 84,87
Weisbord (1971) 52,53,59,65,69,70,74,76,86–88
Weisbord (1973) 52,53,59,60,74,81–84,88
Weisbord (1974) 71
Welch's statistic 69
Wells, J. W. 49,78,80
Wells personal collection 78,80
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Wells (1937) 49
Wells (1956) 60,74
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Wilcoxon 2-sample test 53
Wise, S. 49
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Table 3.—List and description of corallite characters analyzed in *Porites*. Characters 1–2 were measured to the nearest 0.04 mm. Characters 3–5 and 14–25 were measured to the nearest 0.02 mm. Characters 26–29 were measured to the nearest 0.2 mm.

Character	Abbreviation	Description
1. corallite diameter	**CD**	linear measure across corallite center between thecal/corallite cavity margins; average of lengths parallel and perpendicular to dorso-ventral axis
2. corallite spacing	**CS**	linear measure between centers of nearest neighboring corallites; average of longest and shortest lengths
3. septum length (dorsal)	**L1**	linear measure from septum tip to inner thecal margin
4. septum length (ventral)	**L2**	linear measure; see above
5. septum length (lateral)	**L3**	linear measure; see above
6. number of neighboring corallites	**NN**	count
7. total number of septa	**NS**	count
8. number of bifurcated septa	**NB**	count
9. number of denticles/septum	**DS**	count
10. total number of mural denticles	**DW**	count
11. number of pali	**PL**	count
12. number of synapticular rings	**SR**	count
13. number of rows of mural trabeculae	**WR**	count between neighboring corallites
14. septum thickness (dorsal)	**T1**	linear measure across septum at septum midpoint
15. septum thickness (ventral)	**T2**	linear measure; see 14 above
16. septum thickness (lateral)	**T3**	linear measure; see 14 above
17. septal denticle thickness	**SD**	linear measure across denticle (lateral septum) nearest the wall
18. palus thickness (dorsal)	**P1**	linear measure across palus
19. palus thickness (ventral)	**P2**	linear measure; see 18 above
20. palus thickness (lateral)	**P3**	linear measure; see 18 above
21. columella tubercle length	**C1**	linear measure along long axis
22. columella tubercle width	**C2**	linear measure along short axis
23. distance across columellar synapticular ring	**CW**	linear measure; average of longest and shortest distance across ring
24. synapticula thickness	**SY**	linear measure; average of columellar and outermost septal synapticulae
25. wall thickness	**WT**	linear measure between thecal margins of nearest neighboring corallites
26. columella elevation	**CE**	distance estimate using focus knob; from calice base to columella tip
27. pali elevation	**PE**	distance estimate using focus knob; from calice base to pali tips
28. septa elevation	**SE**	distance estimate using focus knob; from calice base to septal denticle tips
29. total calice elevation	**WE**	distance estimate using focus knob; from calice base to uppermost mural trabeculae

Table 4.—List and description of corallite characters analyzed in *Goniopora*. Characters 1–2 were measured to the nearest 0.04 mm. Characters 3–5 and 15–25 were measured to the nearest 0.02 mm. Characters 26–29 were measured to the nearest 0.2 mm.

Character	Abbreviation	Description
1. corallite diameter	**CD**	linear measure; see Table 3
2. corallite spacing	**CS**	linear measure; see Table 3
3. septum length (1st cycle)	**L1**	linear measure from septum tip to inner thecal margin
4. septum length (2nd cycle)	**L2**	linear measure; see 3 above
5. septum length (3rd cycle)	**L3**	linear measure; see 3 above
6. number of neighboring corallites	**NN**	count; see Table 3
7. total number of septa	**NS**	count; see Table 3
8. number of primary septa fused with secondary septa	**F1**	count
9. number of secondary septa fused with tertiary septa	**F2**	count
10. number of denticles/septum	**DS**	count; see Table 3
11. total number of mural denticles	**DW**	count; see Table 3
12. number of pali	**PL**	count; see Table 3
13. number of synapticular rings	**SR**	count; see Table 3
14. number of rows of mural trabeculae	**WR**	count; see Table 3
15. septum thickness (1st cycle)	**T1**	linear measure across septum at septum midpoint
16. septum thickness (2nd cycle)	**T2**	linear measure; see 15 above
17. septum thickness (3rd cycle)	**T3**	linear measure; see 15 above
18. septal denticle thickness	**SD**	linear measure across denticle (primary septum) nearest wall
19. palus thickness (1st septal cycle)	**P1**	linear measure across palus
20. palus thickness (2nd septal cycle)	**P2**	linear measure; see above
21. columella tubercle length	**C1**	linear measure; see Table 3
22. columella tubercle width	**C2**	linear measure; see Table 3
23. total columella width	**CW**	linear measure; average of longest and shortest distance across entire trabecular complex
24. synapticula thickness	**SY**	linear measure; see Table 3
25. wall thickness	**WT**	linear measure; see Table 3
26. columella elevation	**CE**	distance estimate using focus knob; see Table 3
27. pali elevation	**PE**	distance estimate using focus knob; see Table 3
28. septa elevation	**SE**	distance estimate using focus knob; see Table 3
29. total calice elevation	**WE**	distance estimate using focus knob; see Table 3

PREPARATION OF MANUSCRIPTS

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Collinson, J.
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Gilbert Dennison Harris
(1864 - 1952)

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